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SPECIAL PUBLICATION
# of CARNEGIE MUSEUM OF NATURAL HISTORY

PAPERS IN VERTEBRATE PALEONTOLOGY HONORING ROBERT WARREN WILSON

edited by
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Edward O. Wiley
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Jiri Zidek

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* Deceased.

SPECIAL EDITOR'S COMMENTARY

Editing this tribute to my long-time friend and colleague Bob Wilson has been a pleasure on the one hand and an albatross on the other; it has been pleasant interacting with so many of his admirers and co-workers, whom I thank mightily for their patience and good cheer; it has been painful that so many conflicting duties and interruptions have made the job take so long.

For a long time now I have been a bemused observer of vertebrate paleontologists, a perennially small band that has in its history included such unusual individuals as Thomas Jefferson, O. C. Marsh, E. D. Cope, S. W. Williston, W. D. Matthew, and A. S. Romer, to name but a few. The latter-day membership of this calling includes some of my best friends, whose habits I have carefully noted. Perhaps it is time for a preliminary report.

Early, I fell completely in awe of VP's. This may have owed to some extent to eight hours of graduate exposure to Claude ("Hibbie") Hibbard's course in VP, ca. 1950–1951, and subsequent, thankfully brief, experience of the rigors of his fossil camp at Meade County State Park in Kansas. I identified VP's as superhuman composites of stevedore, geologist, comparative anatomist, and evolutionary biologist.

But I was young then. After a time I began to discover that VP's too put on their pants one leg at a time. I learned that, much like mammalogists (and even, I fear, some ornithologists)—every discipline has its own curious profile—they tend to imbibe freely, talk too much, and to lean heavily at times upon aging laurels. No doubt these qualities allied me to them.

Now I have learned that they forget citations, misspell words, and dangle participles just like other people.

Yet perhaps they are to be forgiven. They spend much time in "the field," as they euphemistically term Badwater, Wyoming; Death Valley, California; Ellesmere Island; northeastern Colorado, and comparable garden spots. Nearly all of them incur arthritis, actinic skin damage, chronic sprains, and hernia. They are the desert rats of biological science. Brains baked beneath inadequate pith helmets, backs bowed by too many 100- pound sacks of matrix, eyes sealded by too much sun, who would not become intermittently hallucinogenic? Small wonder that a loan of specimens to a VP is often a lifetime loan, reclaimable (if at all) only after death—assuming the records still exist.

I come at last to a particular specimen of the species, Robert W. Wilson, known to all of the contributors who follow (and to many others) for his thoroughness, caution, erudition, generosity, and seminal contribution to our understanding of rodent evolution. It is to these and other qualities, some of them taken up by his former student "Gabby" Galbreath a bit later, that the participants with obvious affection have dedicated the papers of this "Festschrift." Any further addition of mine to this joyous outpouring would, I fear, embarrass one or both of us, since I see him all the time.

But something more does need to be said, and I cannot think of a better place for its statement.

I refer now to Robert's support system, the late Geraldine Lee Wilson. At first sight an improbable heroine, Gerry masked indomitable strength behind a deceptive facade of flightiness and confusion. She was the nearest thing to a pioneer wife that I shall ever know. While her mate cleansed his spartan soul in the burning wastes, she faced adversity—loneliness, asthmatic children, bills, dishes, and much more—with a will as tough as Jim Bridger's and with irrepressible humor. To her, equally with her fortunate husband, I dedicate the labor that I have gladly put into this volume.

Robert M. Mengel
12 May 1983

Robert W. Wilson

ROBERT WARREN WILSON'S PALEONTOLOGICAL CONTRIBUTION

Larry D. Martin

In a very true sense Robert W. Wilson is one of the pioneers of American vertebrate paleontology. This seems somewhat strange to us here, because he is as active and current now as anyone I am familiar with. His early work, beginning around 1930, covers a remarkable array of famous sites, including such Quaternary localities as the Clovis Mammoth Kill Site in New Mexico, the Carpinteria Tar Pits in California, and Rampart Cave in Arizona. His own field work includes most of the late Miocene sites in the American Southwest, and he is one of the leading students of Miocene biostratigraphy. He has had unusual success as a field paleontologist and this may owe in part to his formal training in geology with Chester Stock. This firm geological background is a qualification that Dr. Wilson shares with such other paleontological notables as W. D. Matthew and G. G. Simpson.

Bob Wilson has always been aware of the importance of comparisons between North America and Eurasia, and this is stressed in his report (1960) on the early Miocene Martin Canyon A Local Fauna. This was the first extensive early Miocene small mammal fauna to be reported from North America and has formed the starting point for later studies of Tertiary microfaunas and faunal exchange with Eurasia. He has continued his work with European and American Miocene biostratigraphy and presently has an extensive research program in Austria where he is a correspondent in the Vienna Museum of Natural History.

Dr. Wilson is one of the founders of small mammal paleontology in North America. I am constantly amazed at how often work on small mammals brings me back to something originally done by Wilson, and how often that work is still the best available on the subject. His work on fossil voles and lemmings is the foundation from which all later workers began, including Claude Hibbard. Wilson's work on fossil rodents has in general been characterized by its broad scope and the strength and durability of his insights. His 1949 paper "Early Tertiary rodents of North America" is a classic, and much of what he proposed in it has since been confirmed. Much of what we now know about such important groups of fossil rodents as the eomyids is a result of Wilson's careful descriptions and interpretations.

The earlier part of the mammalian record has not been neglected by Wilson, and he is presently engaged in research on late Cretaceous mammals from South Dakota and Paleocene mammals from New Mexico. His New Mexico collections are among the most important of that age in the world, and include the oldest known primate skull from North America.

It would be possible to continue at considerable length on Dr. Wilson's successes scientifically and as a collector and teacher. Very few of our colleagues can claim to have done so much, or to have done it so well. But to me the outstanding thing about R. W. Wilson is the generous way he has shared his skill and experience with his students and colleagues. He presently takes time from a very busy retirement schedule to serve on numerous graduate committees. His return to the University of Kansas upon his retirement provides us all with a constant source of advice and information. In fact, if I were asked what was the single most valuable resource in the Division of Vertebrate Paleontology I would without hesitation name Robert W. Wilson.

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REMINISCENCES OF ROBERT WARREN WILSON

E. C. Galbreath

Festschrift organizer Mary Dawson has asked me to record any anecdotes or other observations concerning Bob Wilson that seemed appropriate to this occasion. I have done my best, hoping that I may make up in enthusiasm for the subject whatever I lack in the skill for so demanding a task.

As anyone who knows him in any significant way is aware, Bob Wilson is nothing if not thorough, cautious, and slow to reach conclusions and make pronouncements. The few occasions in which he has been caught off base in some small matter of identification or prediction are therefore cherished trophies in the memories of those former students, or others, fortunate enought to be "in at the kill."

Such a memory, now nostalgically relished by all concerned, was provided by the classic "long-tailed rabbit," a former creature somehow pronounced lagomorph by Robert on the basis of a misleading glance at a partially exposed skeleton. Upon further exposure, this fossil metamorphosed into an unequivocally tailed and clearly entoptychine rodent. It is a mark of true greatness to have an error so distinguished by rarity.

Methodological handmaiden to Robert's caution and conservatism is a benign pessimism that is a way of life with him. Argument with him on this point was inevitably futile in the face of a practised defense that invariably placed the critic in checkmate: namely that pessimists are often rewarded by surprises that are inevitably pleasant and, even more frequently, satisfied by the verification of their predictions and judgments—a no-lose proposition

A case in point occurred when some "big bones" from the Cretaceous Dakota Sandstones of northwestern Kansas required an excursion afield and elicited from Robert characteristic groans and the gloomy prediction that probably nothing would come of it. The trail led to a cattle ford across a stream in a farm field, where some fragments of a large pelvis and vertebrae had been exposed. After some digging these petered out in a huge, amorphous, and very unprepossessing hunk of rock.

Dutifully transported back to the University of Kansas Museum of Natural History—as much to satisfy the public as anything—these dubious items, especially the hunk of rock, were the subject of much banter and joking during which we variously imagined that knobby protuberances from the surface were all kinds of structures, including fossil eyeballs. Nobody really believed the hunk of rock contained anything of consequence until one day much later when Russell Camp in a moment of boredom split the whole thing open. Lo and behold, the "fossil eyeballs" were innocent concretions, as predicted by our sage. But, they were lodged in the orbits of what eventually emerged as a first-rate skull of an ankylosaur. Robert, of course, was pleasantly surprised (again), while the jesters uneasily recalled that, for all of their wit, it was the pessimist who had insisted on lugging the "worthless" hunk of rock all the way back to Lawrence.

This kind of thoroughness in all things is characteristic of the man, who has always insisted that *nothing* be discarded until proved beyond all doubt to the worthless. Such persistence marked all of his field work, exhausting juniors dubious about the value of further fruitless search in this or that locality. One insisted that three weeks with zero return was the absolute minimum for their leader even to consider relocation.

Bob's conservatism in retaining material of dubious value related to another habit that sometimes embarrassed inexperienced students, who at least suspected him of setting sinister educational traps for the unwary. He would often "clean up" a promising exposure by collecting all of the distracting surface litter of scraps and slivers, the better to search for significant veins of more meaningful bone. These scraps he would cache for later retrieval, in piles at the bases of forbs chosen for convenience as markers. There, on occasion, some neophyte would pounce gleefully on a spectacular "find" and then puzzle in mounting frustration as all attempts at meaningful association of its parts failed.

During Robert's tenure at the University of Colorado he and G. Edward Lewis prowled the northeastern part of that state and—with an assist from former K.U. student Curt Hesse—who had drawn a map, possibly from information provided by H. T. Martin—rediscovered the Miocene Martin Canyon locality made famous by W. D. Matthew's work in 1898. At that time Bob located a site that was to be called Quarry A in later years. He, again with characteristic persistence, insisted on its opening, even though one E. C. Galbreath had in his wisdom opined that it was unpromising indeed. This view notwithstanding, the pessimist was pleasantly surprised once more when Quarry A proved to be extremely rich in high grade jaws. It was part of a stream channel with lenses of bone rubble that had served as dams, which had trapped numerous quality elements.

As Quarry A was worked out, in time the path of the channel beyond needed to be traced. At this point the indefatigable Galbreath, encouraged and abetted by one John A. White, conceived the somewhat revolutionary idea that drilling with a posthole auger might be a useful prospecting device. It took a week to convince Bob that this idea was good enough to merit the expenditure of field funds for an auger. With much tom-foolery about witching wands, we drilled several holes that yielded bone scrap, clearly revealed by the sound of the auger grinding through bone. The last hole, as it turned out, produced fragments of bone (scrap, of course), and big pieces of tooth enamel.

At this point the skeptical professor turned instant believer and took command. A little sub-quarry was opened. Good fossil limb bones were exposed and, eventually, a nice rhino skull, remarkable for a four-inch wide, auger-sized hole from the top to and through one tooth-row (as shown in Fig. 3 of D. Yatkola and L. Tanner, 1979, Occas. Papers Mus. Nat. Hist., Univ. Kansas, 77:7). That skull (now an important holotype) and associated elements became known as the "Posthole Rhino" and led to a lot of corny jokes about further auger-battered treasures, all fortunately imaginary. It also led to Bob's absorbing on our behalf some unwarranted criticism from Director E. Raymond Hall concerning the collecting methods Bob had so vigorously opposed for a week.

The auger used at Quarry A returned to haunt Bob Wilson one more time. Our account of the adventure prompted Gerry Wilson to wish wistfully that she had some of those holes in her yard for the clothesline that Bob had promised to erect long ago but somehow had not gotten around to. A little later, in the small hours of the night the original culprits arrived stealthily at the Wilson home equipped with the historic auger and several six-packs of fuel for the operators. Soon the clothesline was installed, whereupon, but not before, Bob Wilson's voice was heard in the darkness announcing that now some loose rock in a nearby retaining wall required immediate attention. He also wished to share in the much-depleted supply of fuel.

On the serious side, for me association with Robert Wilson as his graduate student (and later) was a continuous lesson in intellectual integrity, the importance of logical exposition, and restraint from going beyond the evidence when forming conclusions. In these as in all things he served as a model of kindness, patience, tolerance of differing opinions, consideration, and even forbearance of trespassers. Many of these qualities must have been strained to the utmost while he sought to train me to behave and think in at least a reasonably civilized and satisfactorily effective manner.

His reputation had preceded him before our first meeting. I knew of his work with Chester Stock and other associates at the California Institute of Technology and I was appropriately awed, expecting, no doubt, an Olympian god or a white knight from Camelot. Then one morning there he was: no white knight in aspect—only a lanky, slightly raw-boned, soft-spoken, distinctly reticent, but clearly friendly gentleman.

It was years before I knew much about his formative years or non-professional life, but it was quickly evident that my mentor possessed a broad and superior education not only in science but also in history, literature, music, and other arts. He also revealed a marked fondness for sports, about which he was deeply informed, and detective novels. He played the clarinet well (he had been a trumpet player in his high school band) and had given up chess, which he played well enough to be a member of the formidable Cal Tech chess team, because maintaining the standard of play minimal in his eyes took too much time from more important things.

These things became evident gradually, gently revealed only when called for, and impressed upon me and other students, more than once for the first time, that there was a whole new world of fascinating knowledge to be investigated. We also were subtly led to grasp that opinions based on ignorance revealed much more about the speaker than about the subject.

In summing up, I note that Bob always maintained that—despite claims from some quarters to the contrary—vertebrate paleontology really is an experimental science. It is just that the experiments have all been performed in the variously remote past and many of them buried or lost. But finding the many that still are, or will become, available, predicting the outcomes *a priori*, and fitting predictions to empirical findings, often requires far more ingenuity and patience than pushing things around in the present.

It is perhaps his profound patience, taxing our lesser endowments of that quality, that occasionally moves Bob's students and admirers almost to irritation with this remarkable man.

Once when some then current paleontological controversy was being much debated in the literature I urged Bob to enter the fray—with the details of which he was, as usual, extraordinarily conversant—and set everyone straight. He declined on the basis that he had had his say, and that the disputants would probably come in the end to the same conclusion. In the case in question they did so, but whether or not they later recalled the priority of solution is not that clear. This was and is evidently of far less concern to Bob than to his admirers. Perhaps this is the best measure of all of his superiority.

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BIOGRAPHICAL INFORMATION: ROBERT W. WILSON

MARY R. DAWSON

To some ways of thinking it would be regarded as inadequate and superficial to describe a scientific career that spans more than fifty years with a few biographical highlights. To those accustomed to thinking paleontologically, however, these highlights might be allegorized to fragmentary fossils. From the fossils we reconstruct morphologies, phylogenies, even, at least the more daring of us, whole "scenarios." So from biographical highlights we can reconstruct something of a remarkable career. Here are presented the bare bones, with a few augmentations, of the life of Robert Warren Wilson, the colleague, mentor, and friend to whom this volume is dedicated.

Robert Wilson was born in Oakland, California, on 26 July 1909, third son of Robert Gordon Wilson and Lillie May Silcott. His early interests in geology were developed in high school in Los Angeles, but when he entered the California Institute of Technology it was with the intention of becoming a chemist. Before too long, however, the fascination of geological studies won out. Bob Wilson turned to geology and paleontology, the fields in which he continued all through his studies at Cal Tech. Cal Tech had a strong, progressive geology faculty at that time. From that faculty, the formative influence of Chester Stock was strong and important. Petrographer Ian Campbell and others in varied fields of geology provided him with excellent training. Bob Wilson received the B.S. degree in Science in 1930; M.S. in Geology and Paleontology in 1932; and Ph.D. in 1936, with a major in Vertebrate Paleontology and minor in Petrology (not too many vertebrate paleontologists have a paper on heavy accessory minerals among their publications; see bibliography, 1936). The 1930s were active days in vertebrate paleontology at Cal Tech, with field parties ranging through California, including the Channel Islands, Nevada, Oregon, Idaho, and Wyoming. Active research and publication programs accompanied the field work, as numerous papers including excellent series of papers in Contributions to Paleontology of Carnegie Institution of Washington Publications will attest. Bob Wilson was one of the North American pioneers in specialized studies on fossil rodents and lagomorphs, surprising even his teacher Stock with demonstrations of the paleontologic interest and stratigraphic utility of these then little known parts of the fossil record. The 1930s were bad economic times, but Bob Wilson was supported by Teaching Fellowships from 1930 to 1935 and as Blacker Fellow, 1935 to 1936.

Bob Wilson's first postdoctoral position was as Sterling Research Fellow at Yale University, 1936 to 1937, when he reviewed and revised North American Eocene rodents. Following this he was Research Fellow at Cal Tech for an additional two years, time occupied by his studies on later Eocene rodents of the Sespe Formation as well as on later Tertiary rodents and lagomorphs. He worked as Collaborator-at-large for the National Park Service for a few months in 1939, working on the Quaternary vertebrate fauna of Rampart Cave, Arizona. In 1939 he took up academic duties in the Department of Geology, University of Colorado, where he moved from the rank of Instructor (1939 to 1943) to that of Assistant Professor (1944 to 1946). His Colorado tenure was marked also by a brilliant decision—he married Geraldine Lee on March 20, 1941. From 1946 to 1947 he held a fellowship from the National Research Council, doing research back at Cal Tech. This was an extremely productive time for Bob Wilson, when he wrote important papers on fossil rodents and lagomorphs, including the excellent review, "Early Tertiary Rodents of North America." In 1947 he moved to the University of Kansas, where he served until 1961 as Associate Professor of Zoology and Associate Curator of Vertebrate Paleontology. While there he continued field studies in Colorado, made excellent collections from the Paleocene of New Mexico, and collected also in Kansas, Wyoming, and Utah. For the Wilsons, who by that time included also Bobbie and Margaret, the KU days were full, with students, research, and field work at the university, music, sports, horses, and much more at home. Bob Wilson received a Guggenheim Fellowship for the 1956 to 1957 academic year for work in London, England, and on the Continent dealing with Miocene small mammals and intercontinental correlation.

Bob Wilson became Professor of Paleontology and Director of the Museum of Geology, South Dakota School of Mines and Geology, in 1961. He held these positions until his retirement in 1975. During this interval he conducted field studies in South Dakota and, in 1967 and 1968, was Fulbright Senior Research Scholar at the University of Vienna. His work in Vienna, an outgrowth of his earlier work on intercontinental correlation as shown by Miocene mammals, concentrated on the stratigraphy of the Vienna Basin and Turolian small mammals of the fissures at Kohfidisch, Austria. At the end of this fellowship year in Vienna he attended the XXIII International Geological Congress in Prague. He has the distinction of being one of the few geologists who stayed and even presented a paper on Thursday, August 22, while Russian tanks rumbled in the background. The work in Austria led to continuing studies, many cooperatively with Friedrich Bachmayer at the Naturhistorisches Museum, Vienna, on the Kohfidisch faunas. It also earned Bob Wilson the Arnold Guyot Memorial Award of the National Geographic Society in 1974, led to several study tours as "House Guest" at the Naturhistorisches Museum, and in 1982 brought him the honorary title of Correspondant at that Museum.

For two years following his retirement from South Dakota School of Mines in 1975, Bob Wilson was visiting professor at Texas Tech University. He was invited back to the University of Kansas in 1977 for the Rose Morgan Visiting Professorship. Also in 1977 he was appointed Associate of the Museum of Natural History at the University of Kansas, and became Emeritus Professor there in 1980. In 1981 he spent several months as Senior Fellow at Carnegie Museum of Natural History.

The return to Lawrence, Kansas, for Bob and Gerry was a real homecoming, made still better by having their son Bob and daughter Margaret both working there also. Their enjoyment of the homecoming was all too short, for Gerry lost a valiant battle against cancer in 1981.

Bob Wilson is a Fellow of the Geological Society of America. He is now an Honorary Member of the Society of Vertebrate Paleontology, having been also a charter member of that Society, its Secretary-Treasurer in 1954 and President in 1955. He is a member of the Paleontological Society and the American Society of Mammalogists.

These are the highlights, bare bones perhaps but at least an outline of a distinguished career. It is tempting now to flesh out the bones, but that was the role of Bob Mengel, Larry Martin, and Gaby Galbreath (see previous papers) so I will resign myself to this brief account. To quote our mentor, "Oh well."

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BIBLIOGRAPHY OF ROBERT WARREN WILSON

(excluding some abstracts and similar publications)

1932. *Cosomys,* a new genus of vole from the Pliocene of California. J. Mamm., 13:150–154.

1933. Pleistocene mammalian fauna from the Carpenteria Asphalt. Carnegie Inst. Washington Publ., 440:61–76.

1933. A rodent fauna from later Cenozoic beds of southwestern Idaho. Carnegie Inst. Washington Publ., 440:119–135.

1934. Two rodents and a lagomorph from the Sespe of the Las Posas Hills, California. Carnegie Inst. Washington Publ., 453:13–17.

1934. A new species of *Dipoides* from the Pliocene of eastern Oregon. Carnegie Inst. Washington Publ., 453:21–28.

1935. Cricetine-like rodents from the Sespe Eocene of California. Proc. Nat. Acad. Sci., 21:26–32.

1935. *Simimys,* a new name to replace *Eumysops* Wilson, preoccupied.—a correction. Proc. Nat. Acad. Sci., 21:179–180.

1935. A new species of porcupine from the later Cenozoic of Idaho. J. Mamm., 16:220–222.

1936. A Pliocene rodent fauna from Smiths Valley, Nevada. Carnegie Inst. Washington Publ., 473:17–34.

1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. J. Paleont., 10:388–391 (second author with A. E. Wood).

1936. A new Pleistocene deer-mouse from Santa Rosa Island, California. J. Mamm., 17:408–410.

1936. *Cynomys* near *ludovicianus* (in C. Stock and F. D. Bode. The occurrence of flints and extinct animals in pluvial deposits near Clovis, New Mexico. Part III, Geology and vertebrate paleontology of the late Quaternary near Clovis, New Mexico). Proc. Acad. Nat. Sci. Philadelphia, 88:234–235.

1936. Heavy accessory minerals of the Val Verde Tonalite. Amer. Mineral., 22:122–132.

1937. New middle Pliocene rodent and lagomorph faunas from Oregon and California. Carnegie Inst. Washington Publ., 487:1–19.

1937. Pliocene rodents of western North America. Carnegie Inst. Washington Publ., 487:23–73.

1937. Lagomorpha (in J. R. Schultz. A late Cenozoic vertebrate fauna from the Coso Mountains, Inyo County, California). Carnegie Inst. Washington Publ., 487:106–109.

1937. A new genus of lagomorph from the Pliocene of Mexico. Bull. Southern California Acad. Sci., 36:98–104.

1937. Two Eocene rodents from the Green River Basin, Wyoming. Amer. J. Sci., 34:447–456.

1938. Review of some rodent genera from the Bridger Eocene. Amer. J. Sci., 35:123–137, 207–222, 297–304.

1939. Rodents and lagomorphs of the late Tertiary Avawatz Fauna, California. Carnegie Inst. Washington Publ., 514: 33–38.

1940. California paramyid rodents. Carnegie Inst. Washington Publ., 514:61–83.

1940. Two new Eocene rodents from California. Carnegie Inst. Washington Publ., 514:87–95.

1940. *Pareumys* remains from the later Eocene of California. Carnegie Inst. Washington Publ., 514:99–108.

1940. Rodentia (in R. H. Jahns. Stratigraphy of the easternmost Ventura Basin, California, with a description of a new lower Miocene mammalian fauna from the Tick Canyon Formation). Carnegie Inst. Washington Publ., 514:178–182.

1942. Preliminary study of the fauna of Rampart Cave, Arizona. Carnegie Inst. Washington Publ., 520:171–185.

1942. Rodentia and Lagomorpha (in P. C. Henshaw. A Tertiary mammalian fauna from the San Antonio Mountains near Tonopah, Nevada). Carnegie Inst. Washington Publ., 530: 104–105.

1949. Additional Eocene rodent material from southern California. Carnegie Inst. Washington Publ., 584:3–25.

1949. On some White River fossil rodents. Carnegie Inst. Washington Publ., 584:29–50.

1949. Rodents and lagomorphs of the Upper Sespe. Carnegie Inst. Washington Publ., 584:53–65.

1949. Early Tertiary rodents of North America. Carnegie Inst. Washington Publ., 584:71–164.

1949. Rodents of the Rincon Fauna, western Chihuahua, Mexico. Carnegie Inst. Washington Publ., 584:167–176.

1949. Rodentia (in C. Stock. Mammalian fauna from the Titus Canyon Formation, California). Carnegie Inst. Washington Publ., 584:232–233.

1949. Preliminary report on a Torrejonian faunule from near Angels Peak, San Juan Basin, New Mexico. Bull. Geol. Soc. Amer., 60:1930–1931.

1951. Preliminary survey of a Paleocene faunule from the Angels Peak area, New Mexico. Univ. Kansas Publ., Mus. Nat. Hist., 5:1–11.

1951. Evolution of the early Tertiary rodents. Evolution, 5:207–215.

1953. Fixing of geologic age and position within section. Annex 3 to Professor Hobart M. Smith's letter. Bull. Zool. Nomencl., 8(1–3):43–44.

1953. *Merycoidodon* in the Florissant (in M. D. MacGinitie. Fossil plants of the Florissant Beds, Colorado). Carnegie Inst. Washington Contr. Paleont., 599:74.

1955. Man learned about flying from ancient reptile. Univ. Kansas Alumni Mag., 53:6–7.

1956. Two cases of dental anomaly in early Tertiary mammals. Trans. Kansas Acad. Sci., Winter, 1955, 58(4):514–518.

1956. A new multituberculate from the Paleocene Torrejon fauna of New Mexico. Trans. Kansas Acad. Sci., 59(1):79–84.

1956. The condylarth genus *Ellipsodon.* Univ. Kansas Publ., Mus. Nat. Hist., 9(5):105–116.

1956. Additional remains of the multituberculate genus *Eucosmodon.* Univ. Kansas Publ., Mus. Nat. Hist., 9(6):117–123.

1956. Dental formula in the Muroidea. J. Mamm., 37:295–297.

1960. Early Miocene rodents and insectivores from northeastern Colorado. Univ. Kansas, Paleont. Contrib., Vertebrata, Art. 7, 92 pp.

1961. Review: Malcolm C. McKenna. Fossil mammalia from the early Wasatchian Four Mile Fauna, Eocene of northeastern Colorado. Univ. California Publ. Geol. Sci., 37: 1–130, 1960. J. Paleont., 35:403–404.

1962. The significance of the geological succession of organic

beings: 1859–1959. Univ. Kansas Sci. Bull., Suppl. to vol. 42:157–178.

1963. Notes on North American species of *Heterosorex* Gaillard. Proc. South Dakota Acad. Sci., 42:79–83.

1964. Role of the Museum of Natural History. 1, News, Junior Acad. Sci., South Dakota Acad. Sci., 3:3.

1964. Late Cretaceous mammals from South Dakota. Proc. South Dakota Acad. Sci., 43:210 (abstract).

1965. Type localities of Cope's Cretaceous mammals. Proc. South Dakota Acad. Sci., 44:88–90.

1966. A first record of an alligator from the middle Oligocene of the Big Badlands of South Dakota. Proc. South Dakota Acad. Sci., 45:287–288 (abstract: first author with B. E. Tucholke).

1967. Fossil mammals in Tertiary correlations. Pp. 590–606 *in* Essays in paleontology and stratigraphy, Raymond C. Moore commemorative volume. Dept. Geol. Spec. Publ. 2, Univ. Kansas.

1968. Insectivores, rodents and intercontinental correlation of the Miocene. XXIII Internatl. Geol. Congr. Report, Czechoslovakia, 10:19–25.

1971. Small mammals (Insectivora, Chiroptera, Lagomorpha, Rodentia) from the Kohfidisch Fissures of Burgenland, Austria. Ann. Naturhist. Mus. Wien, 74:533–587, 1970–1971 (second author with F. Bachmayer).

1971. Recovery of small mammals from the Oligocene of western South Dakota. Natl. Geogr. Soc. Res. Reports, 1965 Projects:279–287.

1972. New paromomyid primate from Middle Paleocene Beds, Kutz Canyon area, San Juan Basin, New Mexico. Amer. Mus. Novit., no. 2499:1–18 (first author with F. S. Szalay).

1972. Evolution and extinction in early Tertiary rodents. XXIV Intern. Geol. Congr., Canada, Sect. 7:217–224.

1972. Fossil vertebrates in the United States: a report of the Ad hoc Committee of the Society of Vertebrate Paleontology on the status of fossil vertebrate conservation in the United States. W. Langston, Jr. (chairman), R. L. Carroll, C. L. Gazin, J. A. Lillegraven, T. H. Patton, A. S. Romer, R. W. Wilson: iii + 154 pp.

1975. The National Geographic Society—South Dakota School of Mines and Technology expedition into the Big Badlands of South Dakota, 1940. Natl. Geogr. Soc. Res. Reports, 1890–1954 Projects, 79–85.

1975. Analysis of *Simimys simplex*, an Eocene rodent (?Zapodidae). J. Paleont., 49:856–874 (second author with J. A. Lillegraven).

1977. Fossil vertebrates in the United States: the next ten years. A report of the Society of Vertebrate Paleontology advisory committee for systematics resources in vertebrate paleontology. W. Langston, Jr. (chairman), C. C. Black, J. A. Lillegraven, T. H. Patton, B. Schaeffer, R. W. Wilson: v + 40 pp.

1978. The National Geographic Society—South Dakota School of Mines and Technology expedition into the Poleslide Member of the Big Badlands of South Dakota, 1969: a program of conservation collecting. Natl. Geogr. Soc. Res. Reports, 1969 Reports:637–642.

1978. A second contribution to the small fauna of Kohfidisch, Austria. Ann. Naturhist. Mus. Wien, 81:129–161 (second author with F. Bachmayer).

1978. Type locality of the giant rodent *Manitsha tanka* Simpson (Protrogomorpha, Paramyidae). Occas. Papers, Mus. Texas Tech Univ., no. 52:1–5 (first author with J. A. Lillegraven).

1980. The stratigraphic sequence of North American rodent faunas. Palaeovertebrata, Mem. Jubil. R. Lavocat:273–283.

1980. A third contribution to the fossil small mammal fauna of Kohfidisch (Burgenland) Austria. Ann. Naturhist. Mus. Wien, 83:351–386 (second author with F. Bachmayer).

1982. Biologic and geologic relationships of small fossil mammals in Austria, with special attention to those of Kohfidisch. Natl. Geogr. Soc. Res. Reports, 14:695–709.

1983. Tertiary Gliridae (Dormice) of Austria. Ann. Naturhist. Mus., Wien, 85:129–134 (second author with F. Bachmayer).

1983. Late Cretaceous mammals of western South Dakota, 1974. Natl. Geogr. Soc. Res. Repts., 15:749–752.

PARANYCTOIDES MALEFICUS (NEW SPECIES), AN EARLY EUTHERIAN MAMMAL FROM THE CRETACEOUS OF ALBERTA

RICHARD C. FOX

ABSTRACT

A new species of the Cretaceous lipotyphlan insectivoran *Paranyctoides* is described from parts of the upper and lower dentition discovered in the upper member of the Milk River Formation, Alberta. The upper molars of this new species show a mixture of primitive (wide stylar shelves and large parastylar lobes, for example) and advanced (including coronal outlines, reduced stylocone and preparacrista, strong conules, anterior and posterior protoconal cingula) features that most closely resemble molar features of primitive nyctitheriid lipotyphlans, such as *Leptacodon,* and primitive condylarths, such as *Protungulatum.* These resemblances may indicate that a cohort Ferungulata (for creodonts, carnivorans, and "ungulates" thought to have been monophyletically descended from a Cretaceous palaeoryctid or, at least, palaeoryctoid eutherian) is no longer tenable as a natural group. *Paranyctoides* is not likely to have been a descendant of the Asiatic *Kennalestes,* and seems not close to other Cretaceous leptictoids, or to palaeoryctoids, zalambdalestids, or the enigmatic *Gallolestes.*

INTRODUCTION

In 1970, the first discovered occurrence of apparent lipotyphlan insectivorans in the Mesozoic—from the early Campanian upper member of the Milk River Formation, Alberta—was announced (Fox, 1970). The impact of that discovery was slight, however, receiving notice in Clemens (1973*b*, 1974), Krishtalka (1976*a*), Sigé (1976), Butler (1977), and Kielan-Jaworowska, Bown, and Lillegraven (1979), but not in more comprehensive works concerning early Eutheria, such as those by Kielan-Jaworowska (1975*a*, 1975*b*), McKenna (1975), Szalay (1976), and Crompton and Kielan-Jaworowska (1978). Subsequent to 1970, additional specimens of the Milk River insectivoran were collected, as well as somewhat younger fossils belonging to a closely related species, from the middle Campanian Oldman Formation, Alberta. The latter species, known from parts of the lower dentition, has been named *Paranyctoides sternbergi,* and was included in a review of eutherian mammals from the Oldman Formation (Fox, 1979). The former, the Milk River lipotyphlan, is known both from upper and lower teeth, and comprises a second species of *Paranyctoides.* I describe this species below and examine further (see Fox, 1979) the implications of *Paranyctoides* for clarifying aspects of early eutherian history.

SYSTEMATIC PALEONTOLOGY

Subclass Theria Parker and Haswell 1897
Infraclass Eutheria Gill 1872
Order Insectivora Illiger 1811
Suborder Lipotyphla Haeckel 1866
Superfamily Erinaceoidea
(Fischer von Waldheim 1817)
cf. Family Nyctitheriidae Simpson 1928

Genus ***Paranyctoides*** Fox 1979
Paranyctoides maleficus Fox, new species
(Figs. 1–4, Table 1)

Note.—The classification of the Nyctitheriidae is in dispute: Sigé (1976) allied them with what are here termed the Erinaceoidea; Krishtalka (1976*b*) associated them with the Soricoidea; and Van Valen (1978) included nyctitheres as a subfamily within the Family Adapisoricidae, Suborder Erinaceota (see Van Valen, 1967).

Etymology.—Latin *Maleficus,* adjective, meaning mischievous, in reference to the implications of the species for widely accepted theories of early eutherian evolution.

Holotype.—UA 5573, incomplete left dentary having m2–3.

Referred specimens.—p4: UA 16174; m1: UA 5572, 16170–1, 16175, 16181; m2: UA 5571; m3: UA 16176–7; dentary having m1–2: UA 16168; upper molars: UA 5520, 16169, 16172–3, 16178–80.

Horizon and type locality.—From the upper member of the Milk River Formation, exposed in Verdigris Coulee, approximately 29 km (18 mi) E of the village of Milk River, Alberta. Exact locality data on file at the Laboratory for Vertebrate Paleontology, The University of Alberta, are available to qualified investigators.

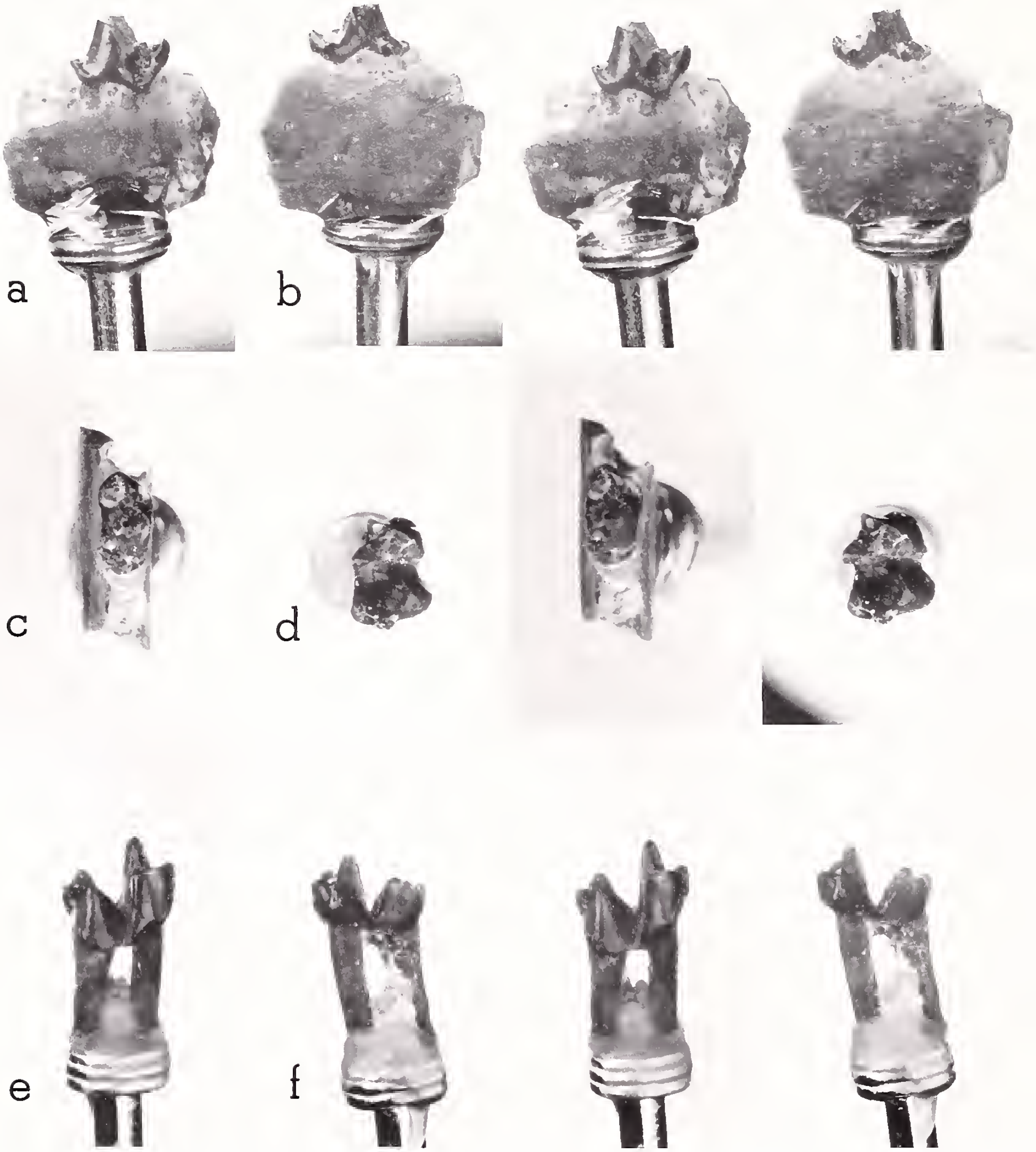


Fig. 1.—*Paranyctoides maleficus* n.sp., Upper Milk River Formation, Alberta. UA 16174, incomplete left dentary having P_4 (protoconid broken): a) labial, b) lingual, c) occlusal, views. UA 16175, right M_1 (protoconid broken): d) occlusal, e) labial, f) lingual, views. Stereophoto pairs, about ×10.

Known distribution.—Upper member, Milk River Formation, Alberta.

Diagnosis.—A species of *Paranyctoides* closely resembling *P. sternbergi* from the Oldman Formation (Fox, 1979), but differing in more robust construction of crowns in comparable parts of lower dentition; upper molars not very transverse, having wide stylar shelf, strong parastylar lobe, weak stylocone, separate paracone and metacone, robust conules, and pre- and postprotoconal cingula, with incipient hypocone on at least some teeth.

Lower Dentition

Knowledge of the lower molar dentition of *Paranyctoides maleficus* is best gained from the type specimen, UA 5573, a fragment of left dentary con-

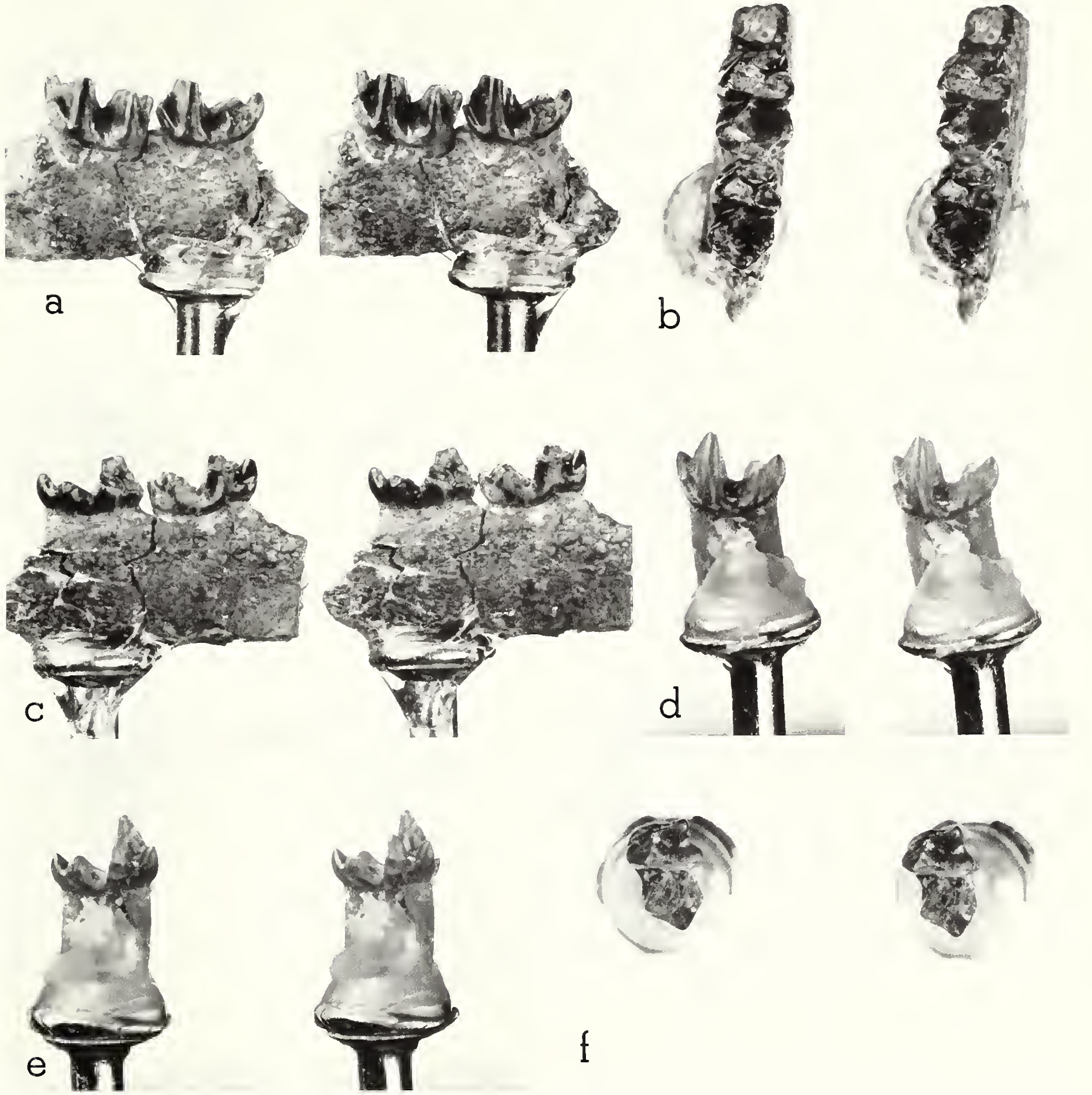


Fig. 2.—*Paranyctoides maleficus* n.sp., Upper Milk River Formation, Alberta. UA 5573, type, incomplete left dentary having M_{2-3} (protoconids and metaconids broken): a) labial, b) occlusal, c) lingual, views. UA 16176, LM_3: d) labial, e) lingual, f) occlusal, views. Stereophoto pairs, about ×10.

taining m2–3 and the alveolus for the posterior root of m1. The other lower molars in the collection at hand are referred to *P. maleficus* from their resemblance to teeth on this specimen. All are closely similar to the molars of *P. sternbergi* from the Oldman Formation.

Ultimate lower premolar.—The term "ultimate premolar" is used here to focus on the uncertainty regarding the homologies of teeth at this position (conventionally called "dp4" and "p4") among eutherians (see, for example, McKenna, 1975; Krishtalka, 1976*a*; Schwartz, 1978; Fox, 1983).

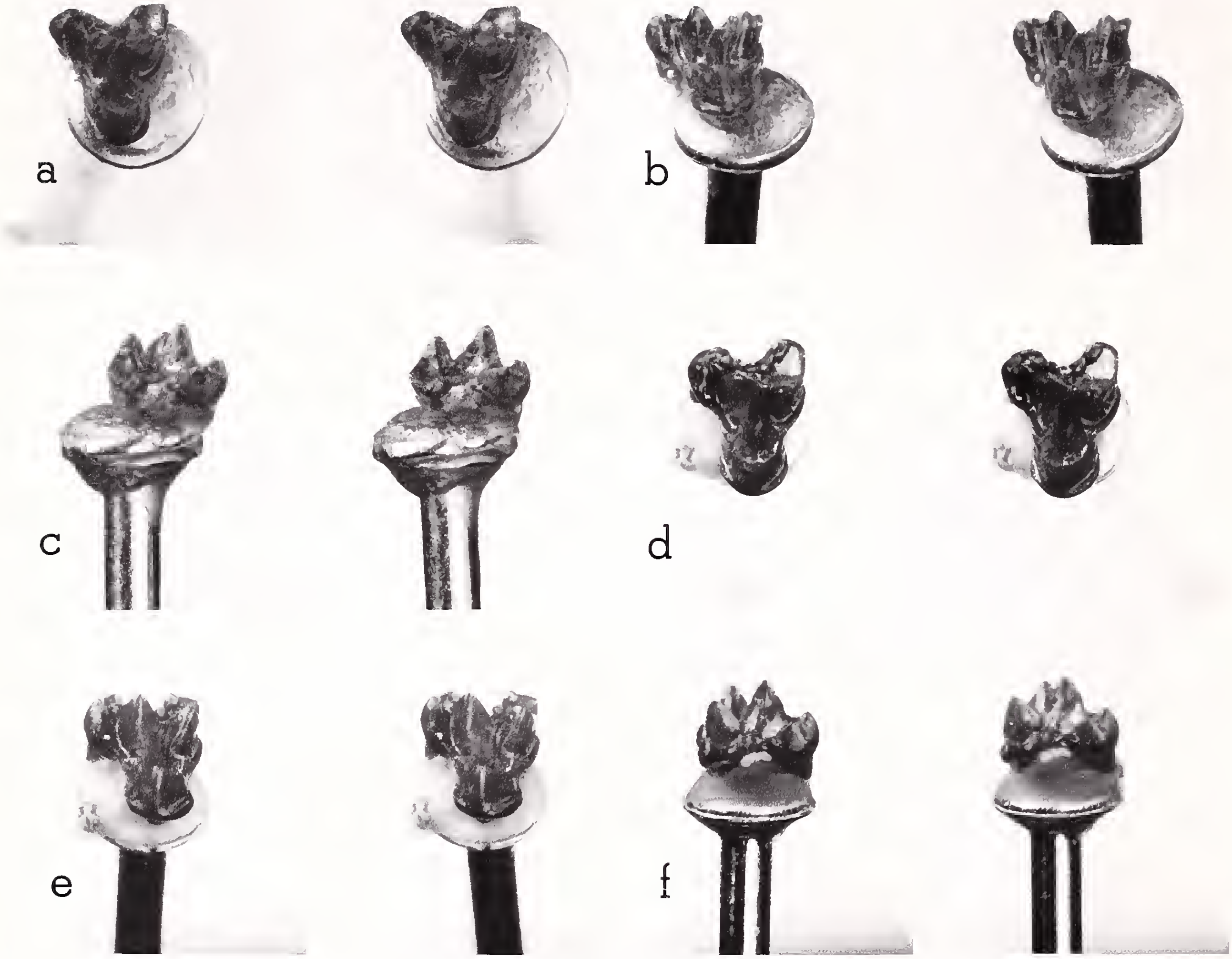


Fig. 3.—*Paranyctoides maleficus* n.sp., Upper Milk River Formation, Alberta. UA 16169, LM^x: a) occlusal, b) lingual, c) labial, views. UA 16172, LM^x: d) occlusal, e) lingual, f) labial, views. Stereophoto pairs, about ×10.

The ultimate lower premolar of *P. maleficus* is known from UA 16174, contained in a fragment of left dentary. The tooth is damaged and incomplete—the apices of the protoconid and paraconid are broken away—but in parts that remain, it is closely similar to the ultimate premolar in *P. sternbergi,* differing in that the talonid basin is broader than in the younger species (although only a hypoconulid is present), the crown is broader in maximum transverse diameter, a labial cingulid is scarcely developed, and a slight swelling is present in the position of a metaconid. A nutritive foramen opens externally on the dentary beneath the anterior root of the premolar, and a second foramen opens externally beneath its posterior root. A foramen in the latter position, but not the former, is known to occur in *P. sternbergi.*

Lower molars.—The lower molars of *Paranyctoides maleficus* correspond closely with those of *P. sternbergi,* with the major differences being the slightly larger size and more robust construction of the crowns, which confers on them a somewhat swollen appearance. As in *P. sternbergi,* trigonids are low relative to talonids, paraconids arise well

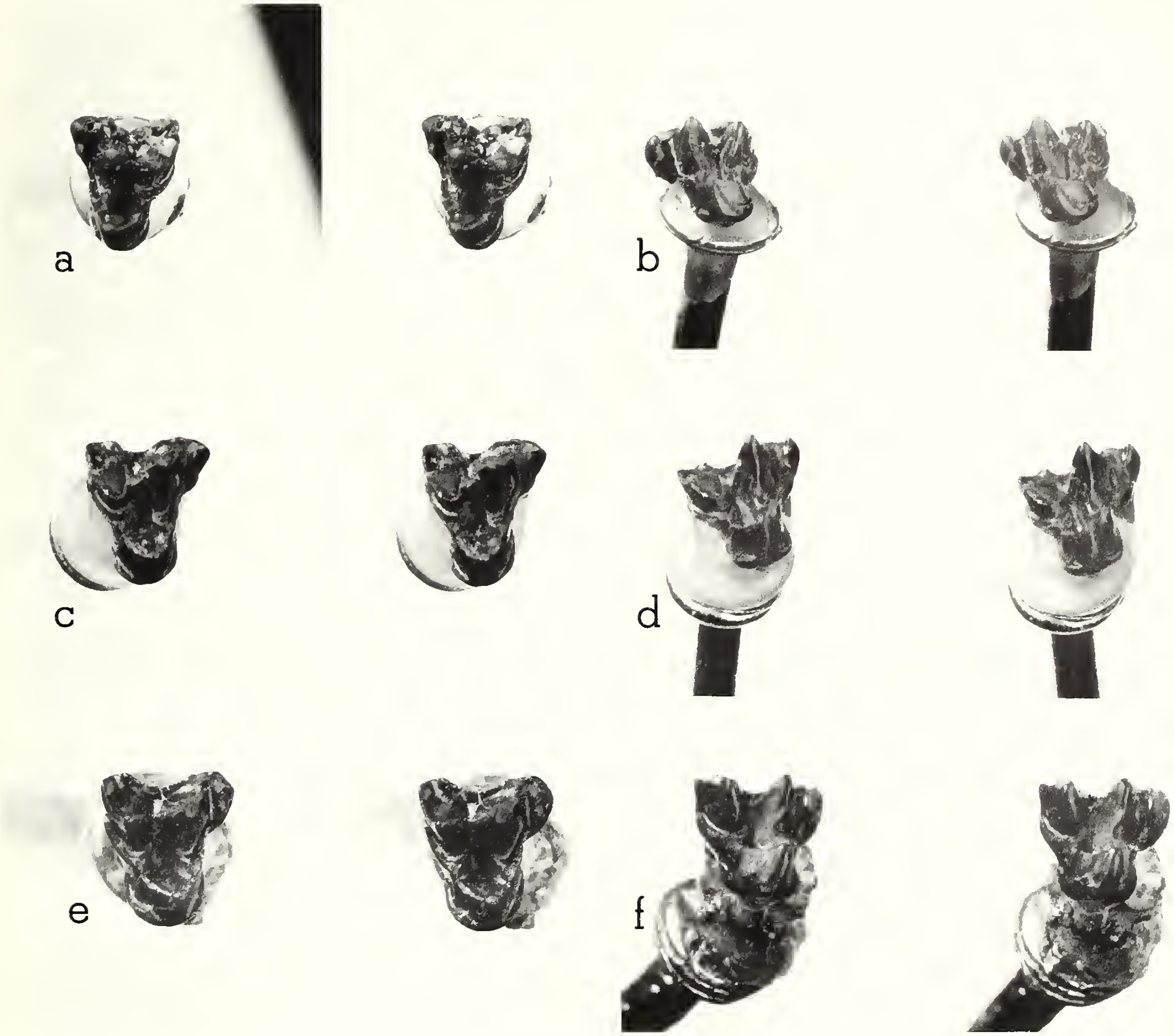


Fig. 4.—*Paranyctoides maleficus* n.sp., Upper Milk River Formation, Alberta. UA 16180, LM^x: a) occlusal, b) lingual, views. UA 16173, RM^x: c) occlusal, d) lingual, views. UA 5520, RM^x: e) occlusal, f) lingual, views. Stereophoto pairs, about ×10.

down on anterior trigonid wall, particularly on m1; talonids are wide and hypoconids broad on m1–2, entoconids are hypoconulids are not "twinned" as in Cretaceous marsupials, and hypoconulid on m3 is a strongly projecting, finger-like cusp. Resemblances in lower molar construction are near enough to suggest a close relationship between *P. maleficus* and *P. sternbergi.*

Upper Dentition

The upper dentition of *Paranyctoides maleficus* is known only from isolated molars. In the collection at hand, teeth representing two positions, M1 and M2, may be present, although observed differences in coronal shape are too subtle to settle the matter decisively. The description below is based, then, on features abstracted from the entire sample, and particular features possibly owing to differences in position are noted thereafter. The identification of upper molars as belonging to *Paranyctoides maleficus* stems from the fit of occlusal patterns with those of the lower molars referred to the species.

Upper molars.—Stylar shelf wide labial to metacone and narrowing anteriorly at level of paracone.

Table 1.—Paranyctoides maleficus *n. sp., Upper member of Milk River Formation, Alberta: dental dimensions.*

Tooth and museum no.	L	Tri	W	Tal
P_4				
UA 16174	1.4		.8	
M_1				
UA 16168	1.6	1.0		1.1
16170	1.5	.8		.9
16171	1.5	.7		.9
16175	1.5	.9		1.0
16181	1.6	.9		1.0
M_2				
UA 5573 (type)	1.7	1.1		1.2
M_3				
UA 5573 (type)	1.7	1.1		1.0
16177	1.7	1.1		—
16176	1.6	1.1		.9
M^x				
UA 5520	1.9		2.2	
16169	1.6		1.8	
16172	1.6		2.1	
16173	1.8		2.1	

Ectoflexus nearly symmetrical, deep, and broad. Stylocone small, at labial edge of crown, and slightly in advance of paracone, to which it is linked along a low, anteriorly convex preparacrista. Labial edge of stylar shelf posterior to stylocone having two cuspules: more anterior and smaller placed behind deepest part of ectoflexus; second and larger—the largest stylar cusp—arising at a level slightly posterior to that of metaconal apex. Parastylar lobe robust and supporting large stylar cusp in advance of transverse groove that receives lower molar protoconid. Small cusp, also adjacent to groove, sometimes arising lingual to main parastylar cusp, and still smaller cuspule sometimes arising labial to main parastylar cusp.

Paracone well separated from metacone; both are somewhat flattened on their labial sides. Paracone larger than metacone, extending farther lingually at base, and leaning somewhat anteriorly. Preparacrista short and weak. Metacone leaning somewhat posteriorly; centrocrista straight across notch between paracone and metacone. Postmetacrista low on stylar shelf and extending to posterolabial corner of crown, terminating there in a slight elevation.

Paraconule strong and extending labially to base of paracone. Preparaconular crista an elevated, cutting crest. Paracingulum wide along its length, shearing against posterior wall of trigonid; accordingly, no distal metacristid occurring on lower molars (Fox, 1975). Postparaconular crista a trenchant crest extending from apex of paraconule to base of paracone. Metaconule robust, although smaller and more labially placed than paraconule. Premetaconular crista a low but trenchant crest extending to base of metacone. Postmetaconular crista similarly developed, and extending along posterior side of crown to a level labial to that of metaconal apex.

Trigon basin deep and well defined. Protocone high, lower than metacone, and leaning somewhat anteriorly, but still posterior to level of paraconal apex. External walls or protocone supporting anterior and posterior cingulum. Cingula broad, shelf-like structures; posterior cingulum can be elevated to a point lingual to its mid-length to form incipient hypocone.

Variation occurs in: 1) size of stylocone (absent on UA 16173); 2) size and detailed construction of parastylar lobe; 3) presence of tiny cusuples on rim of ectoflexus anterior to those already noted (UA 16172 shows two such); 4) dimensions of extoflexus; 5) robustness of protoconal cingula and incipient hypocone, the latter clearly present on only one specimen, UA 5520. These variations may be individual, positional, or taxonomic, or some combination of these factors; I do not now find them taxonomically significant.

RELATIONSHIPS BETWEEN THE SPECIES OF *PARANYCTOIDES*

Only two species of *Paranyctoides* are known, *P. sternbergi* and *P. maleficus.* The tooth crowns and the cusps of *P. sternbergi* are more slender, those of *P. maleficus* are more swollen (bunodont); at present, *P. sternbergi* is the younger in its discovered stratigraphic occurrence (the Oldman Formation lies above the Milk River Formation). How are these species related?

For *Paranyctoides,* it is likely that the discovered stratigraphic succession of fossils does not reflect an ancestral-descendant sequence between its two species: in respect to height of cusps and crests, a common trend in evolution of mammalian dentitions is toward an increase in bunodonty, not a decrease, as would be the case if *P. maleficus* were ancestral to *P. sternbergi,* nor does the evidence in the present case demonstrate a decrease in bunodonty independently of stratigraphic succession. Accordingly, the younger species appears to be the structurally more primitive, and *P. sternbergi* and *P. maleficus* are united through descent from an ancestor having *P. sternbergi*-like crowns. This latter hypothesis (approximation of relationships) is testable (that is, can be modified) by the discovery of new fossil evidence, just as the prior hypothesis, that of an ancestor-descendant relationship, was sensitive to and rejected from the evidence at hand.

CHARACTER STATES OF ANCESTRAL EUTHERIANS AND THE PHYLOGENETIC POSITION OF *PARANYCTOIDES*

From comparison of specimens referred to all relevant species, it is possible to develop an hypothesis of character states of upper and lower molars and ultimate premolars in the "ancestral" eutherians. "Relevant species" is, of course, a subjective choice, but includes species discussed in Patterson (1956), Crompton (1971), and Fox (1975), plus information from the Albian therians additional to *Pappotherium* (see Slaughter, 1971; Butler, 1978); and also includes *Kennalestes* (see below), *Zalambdalestes, Asioryctes, Cimolestes, Batodon, Gallolestes, Gypsonictops, Potamotelses,* the Deltatheridiidae, and all of the Cretaceous marsupials. These species together provide a comprehensive array of Late Cretaceous tribosphenic therians adequate for comparison. The hypothetical character states are:

1. Upper molars 3-rooted and moderately transverse in coronal width; major cusps on uppers and lowers high.
2. Stylar shelf wide, ectoflexus deep, especially on M2.
3. Parastylar lobe prominent and hook-like, and bearing at least one cusp.
4. Stylocone well developed, the largest stylar cusp, and linked to paracone by trenchant preparacrista.
5. Metastylar cusp on ectocingulum, lower and smaller than stylocone, and located labial to metacone.
6. Other stylar cusps small, irregular in position and occurrence.
7. Paracone and metacone separate; paracone more nearly erect, larger and higher than metacone, and more lingually extending at base; metacone leaning somewhat posteriorly.
8. Protocone low, small, lacking cingula; protoconal walls not inflated.
9. Conules small, having poorly developed "wings," and set off lingually from bases of paracone and metacone; paraconule larger than metaconule and placed more lingually.
10. Paracingulum continuous anterior to paracone, from preprotoconal crista to parastyle (Fox, 1975).
11. Cusp "c" (Slaughter, 1971) on high postmetacrista.
12. Postmetaconular crista short, not extending to posterolabial corner of crown.
13. Ultimate upper premolar having protocone and lacking metacone.
14. Lower molar trigonids tricuspid, with protoconid highest and paraconid lowest of trigonid cusps; trigonid angle relatively acute (Fox, 1975).
15. Paraconid cuspate, not appressed against metaconid, located slightly internally (labially).
16. Anterior trigonid wall having short, oblique cingulid and a lingal accessory cusp.
17. Posterior wall of trigonid somewhat oblique transversely and lacking distal metacristid (Fox, 1975), in keeping with complete paracingulum on upper molars.
18. Talonid basined, at widest (m2) little wider than trigonid, and tri-cuspate.
19. Hypoconulid approximately equidistant from hypoconid and entoconid, and centrally placed on posterior talonid rim; short postcingulid extending labially from hypoconulid.
20. Hypoconulid on m3 strongly developed, projecting upward in finger-like fashion.
21. Cristid obliqua meeting posterior wall of trigonid lingual to notch between protoconid and metaconid.
22. Ultimate lower premolar having incipient metaconid and incompletely basined talonid, bearing two cusps (hypoconulid and entoconid).
23. M2/m2 largest molars; M3/m3 smaller than M2/m2, but not greatly reduced.

By comparison, *Paranyctoides* is relatively advanced as follows:

1. Reduced transverse width of upper molars relative to length; increased width of lower molars, and of talonids relative to trigonids.
2. Reduced stylocone and preparacrista.
3. Development of anterior and posterior protoconal cingula, and, on some specimens, incipient hypocone.
4. More robust conules, having well developed "wings."
5. Paraconid arising from relatively low position on trigonid.
6. Absence of lingual accessory trigonid cusp.
7. Lowering of major cusps on both upper and lower molars.

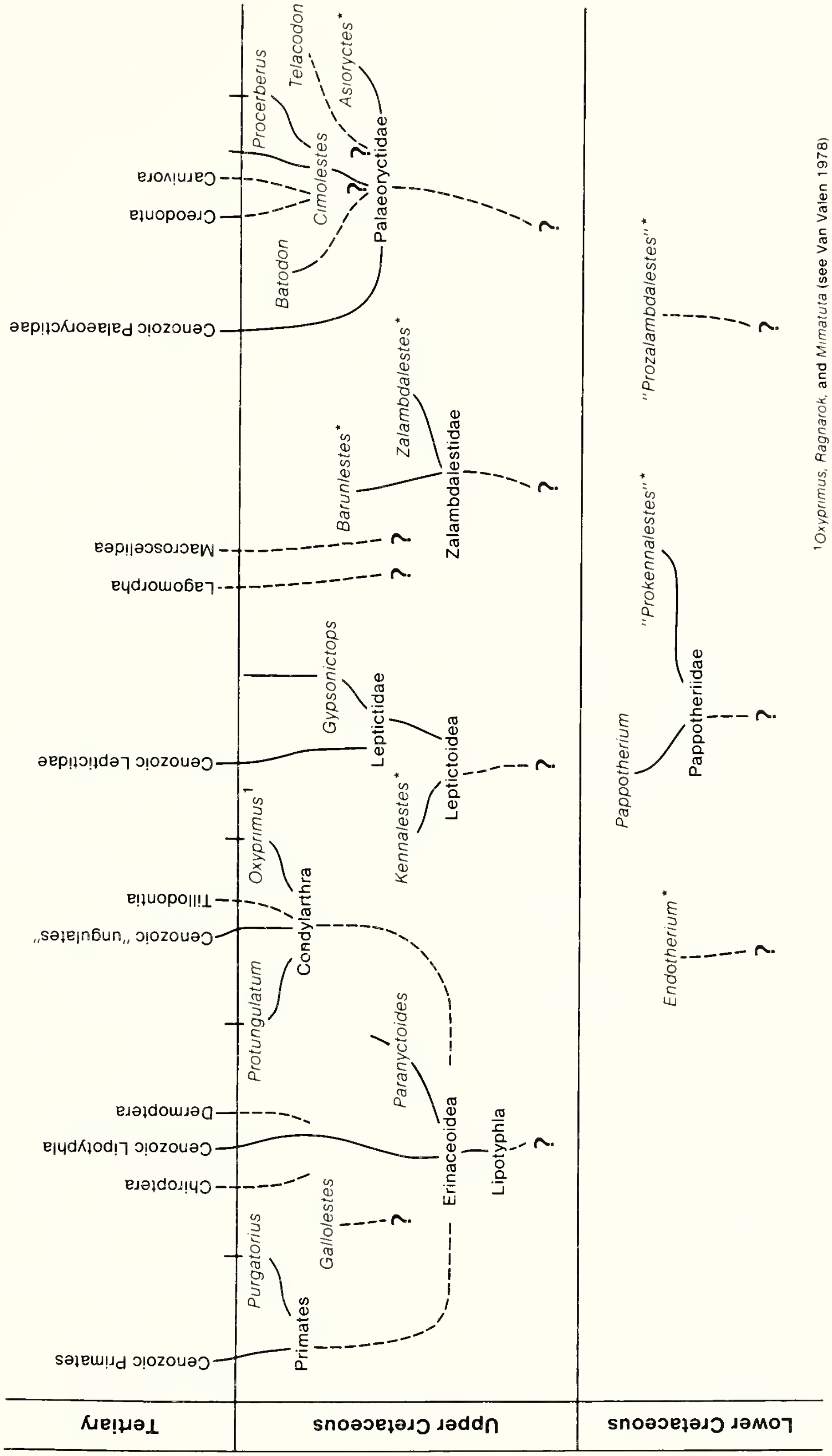
In total, in respect to both primitive and advanced features, the teeth of *Paranyctoides* show greatest resemblances to the teeth of primitive lipotyphlan insectivorans, such as the Paleocene Adapisoricidae and Nyctitheriidae, and primitive protongulate mammals, such as the latest Cretaceous and Paleocene *Protungulatum* Sloan and Van Valen 1965 (and see Fox, 1979). Further, these groups share with *Paranyctoides* each of the presumably advanced features above, except for the low paraconid; major differences in the younger species include relatively narrower stylar shelves, smaller parastylar lobes, and inflated protocones.

Butler (1977; and see Kielan-Jaworowska, Bown, and Lillegraven (1979)) believed that *Paranyctoides* is not "near" any other Cretaceous placental, a view controverted by the illustrations in his own paper. Clearly, the resemblances between the teeth of *Paranyctoides*, lipotyphlans, and primitive condylarths are real; the known differences are no barrier to a close relationship between them (although the position of the paraconid makes it unlikely that *Paranyctoides* itself was ancestral to one or the other of the more progressive groups). No reversals in evolutionary direction are required to explain the resemblances between these groups, and, more positively, the differences observed are bridged by modifications occurring during descent within other lineages of primitive eutherian mammals, and hence are no bar to the relationships suggested here.

More broadly, the importance of *Paranyctoides* resides in its documentation that 1) apparent lipotyphlan mammals having primitive nyctitheriid-like molars existed by middle LateCretaceous time, very much earlier (~20 my) geologically than had previously been known; this is of particular interest in that lipotyphlans, although long recognized to be structurally primitive, had not been discovered at early, Mesozoic horizons; 2) its fossils provide closer structural approximations for groups basal to several higher taxa (including Lipotyphla, Primates, Tupaiidae, Dermoptera, Condylarthra) than any previously suggested alternatives from either the Tertiary or Cretaceous in North America or elsewhere; 3) if *Paranyctoides* is a lipotyphlan and has the relationships to condylarths suggested here, Simpson's (1945) concept of a Cohort Ferungulata (inluding the primarily carnivorous orders Creodonta and Carnivora, plus all of the "ungulate" mammals, and suggested as having descended from Mesozoic eutherians within the Palaeoryctidae—see Lillegraven 1969) needs to be re-examined; 4) North American eutherian mammals of the Mesozoic are not necessarily latest Cretaceous immigrants from other continents; 5) *Kennalestes* (and see below), instead of occupying a central place in early eutherian differentiation (Butler, 1972; Kielan-Jaworowska, 1977; Crompton and Kielan-Jaworowska, 1978), has evolved in specialized, leptictoid directions; and 6) placentals are already diverse in the Late Cretaceous (Butler, 1977), with the genera not being, for the most part, closely related to each other.

PARANYCTOIDES AND *KENNALESTES*

Of known Cretaceous eutherians, *Kennalestes gobiensis* is probably the species most likely to be viewed as relevant to the ancestry of *Paranyctoides*, at least in a structural sense, and perhaps in a phylogenetic sense as well. Kielan-Jaworowska (1969; 1975*a*, 1975*b*; 1977), Lillegraven 1969), Butler (1972, 1977), Clemens (1973*a*), McKenna (1975), and Crompton and Kielan-Jaworowska (1978) have interpreted *Kennalestes* as a very primitive Late Cretaceous eutherian, which it surely is. Kielan-Jaworowska (1975*a*, 1975*b*, 1977), Butler (1972), and Crompton and Kielan-Jaworowska (1978) have gone still further, casting *Kennalestes* in a virtual archetypal role, not only in respect to *Gypsonictops* (Fox, 1977), but to all or nearly all Late Cretaceous eutherians, including *Paranyctoides*. In principle, it is



[1] *Oxyprimus, Ragnarok,* and *Mimatuta* (see Van Valen 1978)

Fig. 5.—Phylogenetic relationships of Cretaceous Eutheria.

doubtful that *Kennalestes* (or any other fossil) can measure up to these latter "responsibilities."

Relative to the upper molars of *Kennalestes,* those of *P. maleficus* are less transverse, have a wider stylar shelf, separate and lower paracone and metacone (partly connate in *Kennalestes*), stronger conules and cristae associated with them, stronger protoconal cingula, weaker stylocone, distal stylar cuspules, lower postmetacrista (although still well developed), stronger parastylar lobe, and weaker ectoflexus. For the lower molars, those of *Paranyctoides* have lower cusps, transversely wider crowns, talonids proportionally wider relative to trigonids, less anteroposteriorly compressed trigonids, and stronger paraconids, arising from a relatively low position on the anterior trigonid wall.

According to present understanding of polarities in the evolution of primitive tribosphenic molars, *Paranyctoides* is more primitive than *Kennalestes* in width of stylar shelf, presence of cuspules on the shelf distal to the stylocone, larger parastylar lobe, fully separate paracone and metacone, and less compressed trigonid and stronger paraconid. *Kennalestes* is the more primitive in occlusal outlines, higher principal cusps, weaker conules, smaller protoconal cingula lacking an incipient hypocone, and higher preparacrista and postmetacrista. The distribution of primitive states in the two forms indicates that *Paranyctoides* is not likely to have been a descendant of *Kennalestes* or a species having a *Kennalestes*-like configuration of the stylar area, paraconids, and ultimate lower premolar (Fox, 1979). Hypotheses of descent of *Kennalestes* from a *Paranyctoides*-like species seem even less compelling (less parsimonious) in terms of what is understood of polarities in molar evolution among Cretaceous Theria; nor is it evident that *Kennalestes* and *Paranyctoides* have some "special" relationship to each other through a close common ancestor, one closer than that between *Kennalestes* and *Gypsonictops,* as one possibility, or even between *Kennalestes* and the Palaeoryctidae, as a second. Nor can it be determined, for example, whether the protoconal cingula in *Kennalestes* and *Paranyctoides* are retentions from a common ancestor or were evolved independently. All one can do at present is to state the likelihood that protoconal cingula are a derived feature, originating at some time after the inception of the Eutheria.

PARANYCTOIDES IN THE CONTEXT OF CRETACEOUS EUTHERIA

The accompanying diagram (Fig. 5) depicts my assessment of the relationships of *Paranyctoides,* other Cretaceous Theria, and the major Cenozoic groups that can be realistically viewed as their descendants (consequently not all eutherian orders are included). Asterisks indicate genera known from Mongolia; the remainder are North American.

I consider *Pappotherium* to be a eutherian. Butler (1978), in keeping with several recent authors (for example, Turnbull, 1971; Kielan-Jaworowska, 1975*b*), does not; nor do Kielan-Jaworowska, Eaton, and Bown (1979). Butler (1978) has restored *Papportherium* with four molars, but he has not shown why tooth fragments that he supposes represent upper molars at anterior positions in *Pappotherium* do not instead pertain to one or another of the now several named tribosphenic therians in the Trinity Sands known from only lower molars. Further, the molars on the type specimen of *Pappotherium* closely resemble undescribed teeth of "Prokennalestes," an undoubted eutherian having three molars, from the Lower Cretaceous of Mongolia (Beliajeva et al. 1974). Slaughter (1981) has reconfirmed the eutherian status of *Pappotherium* on still different grounds.

I follow Clemens (1974), Krishtalka and Schwartz (1978), and Kielan-Jaworowska, Bown, and Lillegraven (1979) in considering *Purgatorius* a primate (but not Schwartz, Tattersall, and Eldredge [1978], who do not). The phylogenetic position of *Gallolestes* is uncertain (Lillegraven, 1976; Butler, 1977); the shape of the crowns perhaps suggests lipotyphlan affinities, but a molariform ultimate premolar (see Krishtalka 1976*a, b*) is unexpected in a primitive lipotyphlan. Kielan-Jaworowska, Bown, and Lillegraven (1979) note some resemblances of *Gallolestes* to palaeoryctids.

Oxyprimus, Ragnarok, Earendil and *Mimatuta* are new condylarths that join *Protungulatum* in the uppermost Cretaceous and Paleocene (Van Valen 1978; Johnston 1980*b*; Archibald 1982); *Ragnarok, Earendil,* and *Mimatuta* are omitted from the chart because of lack of space on it.

I follow Fox (1977) in respect to relationships between *Kennalestes* and *Gypsonictops*; Butler (1977) Crompton and Kielan-Jaworowska (1978) and Kielan-Jaworowska, Bown, and Lillegraven (1979) disagree, but have not taken into account the derived state of the premolar pattern in *Kennalestes* (Fox 1977): failing a reversal in evolution, *Kennalestes* can not be ancestral to *Gypsonictops*, and insofar as it has evolved in leptictoid directions, it is not ancestral to any other eutherian group. I do not consider the possession of five lower premolar loci and other primitive states sufficient to remove *Gypsonictops* from the Leptictidae, thereby differing from Butler (1972) and Novacek (1977).

McKenna (1975, and references therein) and Szalay (1976) associate the lagomorphs and elephant shrews with the Asiatic zalambdalestids, but Kielan-Jaworowska (1979) and Kielan-Jaworowska, Bown, and Lillegraven (1979), from both cranial and postcranial remains, strongly disagree. Kielan-Jaworowska (1975*b*) has shown close affinity between *Zalambdalestes* and *Barunlestes*.

Lillegraven (1969) and Clemens (1973*a*) have best reviewed the relationships of the Palaeoryctidae. New fossils from the Upper Cretacous of Saskatchewan, Canada, strongly corroborate an hypothesis of descent of *Procerberus* from *Cimolestes* (Johnston, 1980*a*), as first argued by Lillegraven (1969). Van Valen (1978) has extended the range of *Procerberus* into the Paleocene.

The relationships of *Telacodon* are uncertain (Clemens, 1973*a*) but may be nearer the Palaeoryctidae than to other groups. *Batodon* has recently been the focus of new interpretations that would ally it with the Lipotyphla (McKenna, 1975; Novacek, 1976), but that view is rejected here. Szalay's (1976) inclusion of Leptictinae and Palaeoryctinae in a single order, and *Asioryctes* in its own separate family as eutherian, *incertae sedis,* does not reflect resemblances in the pertinent fossils and is not followed in this paper.

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LITERATURE CITED

Archibald, J. D. 1982. A study of Mammalia and geology across the Cretaceous-Tertiary boundary in Garfield County, Montana. Univ. California Publ. Geol. Sci., 122:1–286.

Beliajeva, E. E., B. A. Trovimov, and V. J. Reshetov. 1974. General stages in evolution of late Mesozoic and early Tertiary mammalian faunas in Central Asia. Pp. 19–45, *in* Mesozoic and Cenozoic faunas and biostratigraphy of Mongolia (in Russian). Trans. 1.

Butler, P. M. 1972. The problem of insectivore classification. Pp. 253–265, *in* Studies in vertebrate evolution (K. A. Joysey and T. S. Kemp, eds.), Oliver and Boyd, Edinburgh.

———. 1977. Evolutionary radiation of the cheek teeth of Cretaceous placentals. Acta Palaeont. Polonica, 22:241–271.

———. 1978. A new interpretation of the mammalian teeth of tribosphenic pattern from the Albian of Texas. Breviora, 446:1–27.

Clemens, W. A. 1973*a*. Fossil mammals of the type Lance Formation, Wyoming. Part III. Eutheria and summary. Univ. California Publ. Geol. Sci., 94:1–102.

———. 1973*b*. The roles of fossil vertebrates in interpretation of Late Cretaceous stratigraphy of the San Juan Basin, New Mexico. Pp. 154–167, *in* Cretaceous and Tertiary rocks of the southern Colorado Plateau (J. E. Fassett, ed.), Mem. Four Corners Geol. Soc., Durango, Colorado.

———. 1974. *Purgatorius,* an early paromomyid primate (Mammalia). Science, 184:903–905.

Crompton, A. W. 1971. The origin of the tribosphenic molar. Pp. 65–87, *in* Early mammals (D. M. Kermack, ed.), Zool. J. Linnean Soc., Suppl. 1, 50.

Crompton, A. W., and Z. Kielan-Jaworowska. 1978. Molar structure and occlusion in Cretaceous therian mammals. Pp. 250–287, *in* Development, function and evolution of teeth (P. M. Butler and K. A. Joysey, eds.), Academic Press, London.

Fox, R. C. 1970. Eutherian mammal from the early Campanian (Late Cretaceous) of Alberta, Canada. Nature, 227:630–631.

———. 1975. Molar structure and function in the Early Cretaceous mammal *Pappotherium*: evolutionary implications for Mesozoic Theria. Canadian J. Earth Sci., 12:412–442.

———. 1977. Notes on the dentition and relationships of the Late Cretaceous insectivore *Gypsonictops* Simpson. Canadian J. Earth Sci., 14:1823–1831.

———. 1979. Mammals from the Upper Cretaceous Oldman Formation, Alberta. III. Eutheria. Canadian J. Earth Sci., 16:114–125.

———. 1983. Evolutionary implications of tooth replacement in the Paleocene mammal *Pararyctes*. Canadian J. Earth Sci., 20:19–22.

Johnston, P. A. 1980*a*. First record of Mesozoic mammals from Saskatchewan. Canadian J. Earth Sci., 17:512–519.

———. 1980*b*. Latest Cretaceous and early Paleocene mammals from Saskatchewan. Univ. Alberta, unpubl. M. Sc. thesis.

Kielan-Jaworowska, Z. 1969. Preliminary data on the Upper Cretaceous eutherian mammals from Bayn Dzak, Gobi Desert. Palaeont. Polonica, 19:171–191.

———. 1975*a*. Late Cretaceous mammals and dinosaurs from the Gobi Desert. Amer. Sci., 63:150–159.

———. 1975*b*. Preliminary description of two new eutherian genera from the Late Cretaceous of Mongolia. Palaeont. Polonica, 33:5–15.

———. 1977. Evolution of the therian mammals in the Late Cretaceous of Asia. Part II. Postcranial skeleton in *Kennalestes* and *Asioryctes*. Palaeont. Polonica, 37:65–83.

———. 1979. Evolution of the therian mammals in the Late Cretaceous of Asia. Part III. Postcranial skeleton in the Zalambdalestidae. Palaeont. Polonica, 38:3–41.

Kielan-Jaworowska, Z., T. M. Bown, and J. A. Lillegraven. 1979. Eutheria. Pp. 221–258, *in* Mesozoic mammals: the first two-thirds of mammalian history (J. A. Lillegraven, Z. Kielan-Jaworowska, and W. A. Clemens, eds.), Univ. California Press, Berkeley.

Kielan-Jaworowska, Z., J. G. Eaton, and T. M. Bown. 1979. Theria of metatherian-eutherian grade. Pp. 182–191, *in* Mesozoic mammals: the first two-thirds of mammalian history (J. A. Lillegraven, Z. Kielan-Jaworowska, and W. A. Clemens, eds.), Univ. California Press, Berkeley.

Krishtalka, L. 1976*a*. Early Tertiary Adapisoricidae and Erinaceidae (Mammalia, Insectivora) of North America. Bull. Carnegie Mus. Nat. Hist., 1:1–40.

———. 1976*b*. North American Nyctitheriidae (Mammalia, Insectivora). Ann. Carnegie Mus., 46:7–28.

Krishtalka, L., and J. H. Schwartz. 1978. Phylogenetic relationships of plesiadapiform-tarsiiform primates. Ann. Carnegie Mus., 47:515–540.

Lillegraven, J. A. 1969. Latest Cretaceous mammals of upper part of Edmonton Formation of Alberta, Canada, and review of marsupial-placental dichotomy in mammalian evolution. Univ. Kansas Paleont. Contrib., Art. 50:1–22.

———. 1976. A new genus of therian mammal from the Late Cretaceous "El Gallo Formation," Baja California, Mexico. J. Palento., 50:437–443.

McKenna, M. C. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21–46, *in* Phylogeny of the Primates (W. P. Luckett and F. S. Szalay, eds.), Plenum Publ. Corp., New York.

Novacek, M. J. 1976. Insectivora and proteuthria of the later Eocene (Uintan) of San Diego County, California. Contribs. Sci., Nat. Hist. Mus. Los Angeles County, 283:1–52.

———. 1977. A review of Paleocene and Eocene Leptictidae (Eutheria: Mammalia) from North America. Paleobios, 24: 42 pp.

Patterson, B. 1956. Early Cretaceous mammals and the evolution of mammalian molar teeth. Field Mus. Nat. Hist., Fieldiana Geology, 13:1–104.

Schwartz, J. H. 1978. Dental development, homologies, and primate phylogeny. Evolutionary Theory, 4:1–32.

Schwartz, J. H., I. Tattersall, and N. Eldredge. 1978. Phylogeny and classification of the primates revisited. Yearbook Phys. Anthropol., 21:95–133.

Sigé, B. 1976. Insectivores primitifs de l'Eocene Supérieur et Oligocène Inférieur d'Europe Occidentale. Nyctithériidés. Mém. Mus. Nat. d'Hist. Nat., Paris, 34:140 pp.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., 85: 350 pp.

Slaughter, B. H. 1971. Mid-Cretaceous (Albian) therians of the Butler Farm local fauna. Pp. 131–143, *in* Early mammals (D. M. Kermack and K. A. Kermack, eds.), Zool. J. Linnean Soc., Suppl. 1, 50:131–143.

———. 1981. The Trinity therians (Albian, Mid-Cretaceous) as marsupials and placentals. J. Paleont., 55:682–683.

Sloan, R. E., and L. Van Valen. 1965. Cretaceous mammals from Montana. Science, 148:220–227.

Szalay, F. S. 1976. Phylogenetic relationships and a classification of the eutherian Mammalia. Pp. 315–374, *in* Major patterns in vertebrate evolution (M. K. Hecht, P. C. Goody, and B. M. Hecht, eds.), Plenum Press, New York.

Turnbull, W. 1971. The Trinity therians: their bearing on evolution in maruspials and other therians. Pp. 151–179, *in* Dental morphology and evolution (A. A. Dahlberg, eds.), Univ. Chicago Press, Chicago.

Van Valen, L. 1967. New Paleocene insectivores and insectivore classification. Bull. Amer. Mus. Nat. Hist., 135:217–284.

———. 1978. The beginning of the Age of Mammals. Evol. Theory, 4:45–80.

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EARLY EOCENE MULTITUBERCULATES (MAMMALIA: ALLOTHERIA) FROM THE BIGHORN BASIN, WYOMING

Leonard Krishtalka

ABSTRACT

Three species of multituberculates—*Ectypodus tardus*, *Parectypodus* sp., *Neoliotomus ultimus*—are described from early Wasatchian deposits in the Bighorn Basin. One, or possibly two, species of *Ectypodus* survived into the late Eocene and early Oligocene, but the genus remains unknown from Bridgerian horizons.

INTRODUCTION

In 1952 and 1953 J. L. Kay, J. A. Dorr, and a Carnegie Museum of Natural History field party collected three large fossiliferous blocks from two localities in the "Grey Bull horizon" of the Bighorn Basin. Two came from a quarry along Adobe Creek, west of Manderson, Wyoming (CM locality 676), and the third from exposures five miles west of Basin, Wyoming, in Section 21 or 22, T 51N, R 94W (CM locality 681). These blocks yielded a wealth of well preserved condylarth, perissodactyl, artiodactyl, carnivore, creodont, tillodont, insectivore, and multituberculate remains that were never described. Kay and party also collected remains of a variety of small mammals from the surface of nearby exposures in Sections 10–11, T 50N, R 94W (CM locality 150), among them a partial dentary of a multituberculate. The deposits called "Grey Bull horizon" in the field records appear to correspond with the Elk Creek facies of the lower Willwood Formation as defined by Bown (1979).

Abbreviations are as follows: CM, Carnegie Museum of Natural History; PU, Princeton University; L, length; W, width. All measurements in text and tables are in millimeters (mm). The term "relative height of the first serration" of multituberculate P_4s (Sloan, 1966; Holtzman, 1978) is the ratio of the distance between the dorsal lip of the anterobasal concavity and the first serration to the standard length of the tooth.

SYSTEMATICS

Order Multituberculata Cope, 1884
Suborder Ptilodontoidea
(Gregory and Simpson, 1926)
Family Neoplagiaulacidae Ameghino, 1890

Ectypodus Matthew and Granger, 1921
Ectypodus tardus (Jepsen, 1930)
(Fig. 1; Table 1)

Referred specimens.—Partial dentary with: P_4–M_2, CM 12300; I, P_4, CM12117, 17464; P_4, CM 12123, 12131, 12132, 12133, 17465; isolated P_4, CM 12118.

Localities.—CM 676, 681, Elk Creek facies, Willwood Formation, Wyoming.

Known distribution.—Wasatchian of Colorado, Wyoming; Sparnacian of France.

Description: mandible.—CM 17464 is a nearly complete left dentary of which only the labial surface and the mandibular condyle can safely be exposed by preparation. The coronoid process and part of the corpus of the mandible below the ascending ramus are not preserved. In labial view, the ventral border of the mandible is gently convex from the incisor alveolus to a point below the beginning of the ascending ramus, and is more nearly straight from that point to the back corner of the jaw. The posterior margin below the condyle is straight and vertical; the posteroventral corner is rounded. A raised lip at this corner delimits the margins of a shallow masseteric fossa. There is no angular process. The posterodorsal corner of the condylar process is also rounded, whereas its anterodorsal corner is a sharp-edged right angle. The vertical anterior and horizontal dorsal margins of the condylar process are parallel respectively to the posterior and ventral borders of the jaw. The anterior part of the condylar process is approximately 20% higher than the corpus of the mandible just anterior to the process. In end view the base of the dentary is narrow but the jaw becomes broader dorsally as its labial and lingual walls diverge to form the condyle. The superior surface of the condyle (1.8 mm greatest width in end view) is not perpendicular to the ver-

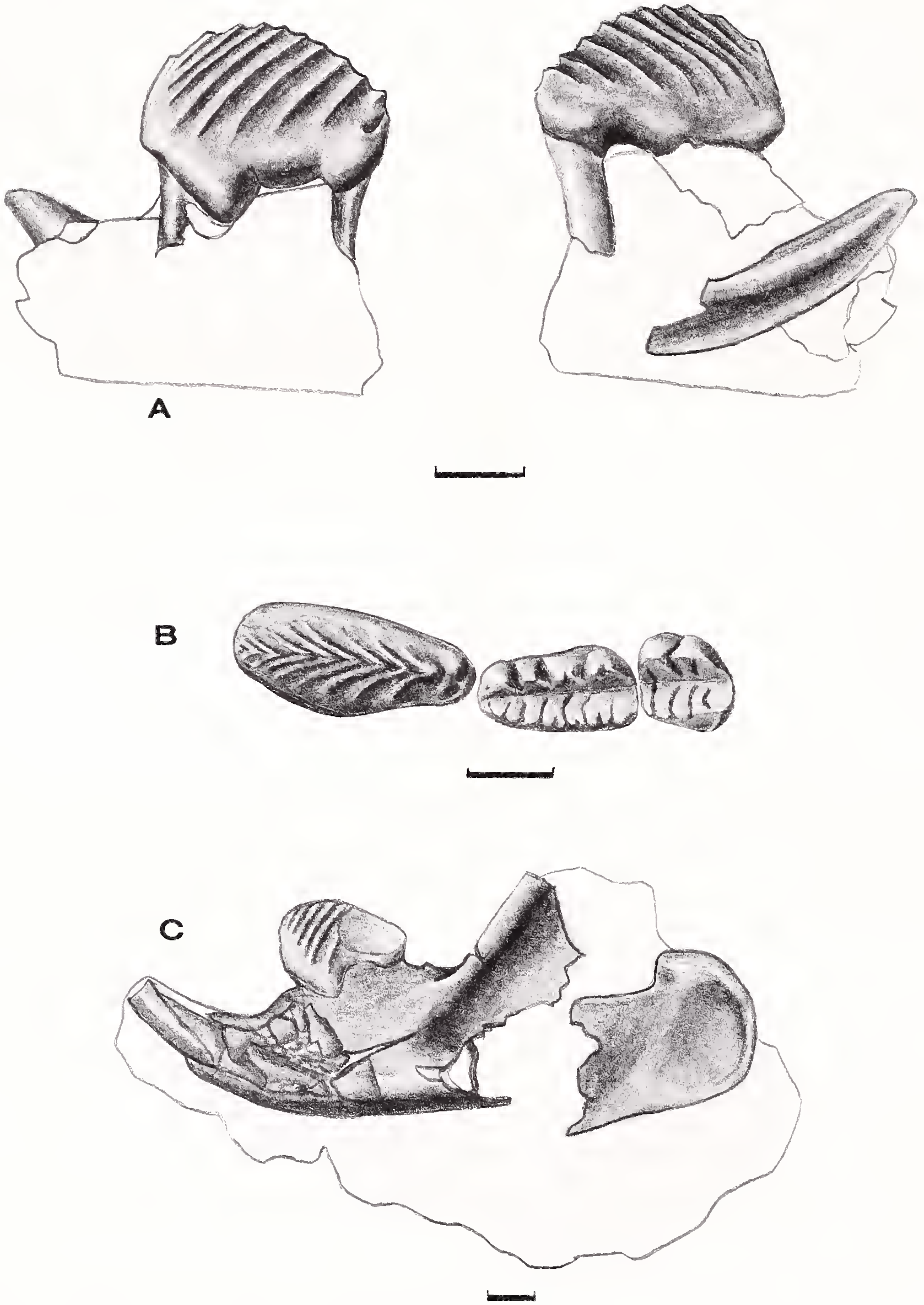

Fig. 1.—*Ectypodus tardus.* A. CM 12117, left I, P$_4$; labial and lingual views. B. CM 12300, left P$_4$–M$_2$; occlusal view. C. CM 17464, left dentary with I, P$_4$; labial view. Scale indicates one mm.

tical posterior border of the jaw, but slopes gently from its higher internal edge to the lower external one. From posterodorsal aspect the condylar area resembles a rounded teardrop with a long basal stem; in dorsal view it is more nearly circular (1.7 mm diameter).

Incisor.—Both of the lower incisors in this sample occur in association with a P$_4$. On CM 12117, a partial left dentary perhaps of a juvenile individual, the anterior part of a left lower incisor is preserved in the dentary below P_4, with the tip erupted just anterior to the premolar. The incisor, extremely compressed, is divided into external and internal surfaces by crests that meet at the tip. The external surface, of which only the anteriormost part is exposed, is gently convex in cross-section. The internal face is subdivided longitudinally into two surfaces by a weak ridge that runs posteriorly from the tip. Both of these surfaces are shallowly concave, with the labial one approximately half as wide as the lingual one.

On CM 17464 the posterior part of a lower incisor is exposed by breakeage on the labial surface of the dentary posteriorly to below the anterior root of P_4. The incisor is slightly laterally compressed and its broken anterior end is ovoid in cross-section. Enamel completely covers the surface of both incisors.

P_4.—P_4 (L, 2.7–3.0 mm) bears 10 (5 specimens) or 11 (3 specimens) serrations that become progressively stronger posteriorly. The relative height of the first serration is 0.34–0.40 and the third or fourth serration is highest above the line for standard length. The profile, higher anteriorly than posteriorly, is convex between the first and either the fifth or sixth serrations, and more nearly straight and posteroventrally inclined from the latter to the last serration. The interserration distance becomes progressively smaller from the first to fifth or sixth serrations, and is approximately equal thereafter. The leading edge of the blade is either straight or barely convex between the anterobasal concavity and the first serration. On those P_4's with the latter condition, only the upper one-third of the leading edge is arcuate.

The labial and lingual ridges from the first serration are either absent or barely discernable, as is also the last lingual ridge. Those from the second serration are weak, but the posterior ridges become progressively stronger and more widely spaced. The longest labial ridges—those from the third to seventh serrations—end on or just above the exodaenodont lobe. Four of the blades (CM 12132, 12133, 12300, 17464) have a second lingual ridge that runs posteroventrally from the penultimate serration. This occurs on two other P_4's (CM 12131, 12123) but is further modified in that the posterior ridge runs ventrally and bifurcates into anterior and posterior branches. On CM 12300 two labial grooves curve posteroventrally, one from between the last and penultimate serration, and the other from between the latter and the antepenultimate serration. This does not occur on CM 12117 and is not observable on the other blades because of excessive wear.

Table 1.—*Dimensions of P_4's of* Ectypodus tardus.

Specimen	Length	Serrations	Rel. ht. 1st serration
CM 12123	3.0	10	0.40
CM 12300	2.7	10	0.37
CM 17465	2.7	10	0.37
CM 12131	2.7	10	0.35
CM 12132	2.7	11	0.35
CM 12133	2.8	11	0.39
CM 12117	2.8	10	0.34
CM 17464	2.8+	11	0.38

On the seven specimens that preserve the dentary anterior to P_4 there is no indication of a P_3 or an alveolus for that tooth. All of the blades, however, have a shallow anterobasal depression in that portion of the leading edge that overhangs the anterior root. The anterior root, exposed on two of the P_4's (CM 12117, 17465), bears a shallow vertical groove on its anterior face that is continuous with the anterobasal depression. In the single specimen with P_4–M_2 the crown of the premolar is aligned with the internal row of cusps on the molars.

M_{1-2}.—The only molars in the sample occur in association with P_4 in a partial left dentary (CM 12300). On M_1 (L, 1.7; W, 0.8; cusp formula, 7:4) the two rows of cusps diverge posteriorly from the anterior edge of the crown to the level of the third external cusp, but are more nearly parallel posteriorly. The lingual margin of the crown is slightly emarginate between the second and third internal cusps, and the crown is widest at the level of the last internal cusp. The posterior border is oriented posterolabially. In the external row the first cusp is smallest, the second larger, the third to sixth cusps subequal and larger than the second, and the last cusp largest. The external cusps, especially the first three, are lower and more worn than the internal ones. In the internal row the first cusp is triangular, whereas the other three are four-sided. The second internal cusp is highest and least worn.

The lateral margins of the crown of M_2 (L, 1.0; W, 0.9; cusp forumla, 4:2) are parallel and the posterior border is oriented posterolabially because of the longer external row. As on M_1, the external row on M_2 is heavily worn and the four cusps are ill-defined. The two internal cusps, higher and larger than the external ones, are clearly separated by a deep notch. Each bears a deep vertical groove on its medial face and a large wear facet on its lateral one.

Remarks.—All of the P_4's discussed here exhibit a profile typical of *Ectypodus*: higher and more arcuate anteriorly than posteriorly; a more nearly straight than convex leading edge; a relative height of the first serration (0.34–0.40) and an anterior profile that are lower than those of *Parectypodus* and higher than those of *Mesodma*; the third or fourth serration is highest above the line for standard length. On P_4's of *Neoplagiaulax* the fifth, sixth, or seventh serrations are highest and the posterolabial ridges are reversely oriented (Krause, 1977; Holtzman, 1978; Sloan, 1981).

Among known species of *Ectypodus*, this material most closely resembles comparable parts of the dentition of the Wasatchian *E. tardus* and the Tiffanian *E. powelli*. Both species, according to published descriptions (Jepsen, 1930, 1940; McKenna, 1960) are similar in size, number of serrations on P_4 (9–11, *E. tardus*; 10, *E. powelli*), lower molar cusp formula (M_1, 7–8:4; M_2, 4:2), and, until most recently, were thought to lack P_3. Sloan (1979) figured a P_3 in an illustration of *E. tardus* and has shown (Sloan, 1981) that its occurrence, as well as the anterobasal depression on P_4 is variable. One possibly distinguishing feature—a different cusp formula on M^1 (7:7:7, *E. powelli*; 8:9:6, *E. tardus*)—is no longer valid: identification of the only known complete M^1 of *E. powelli* (PU 14463) was tentative (Jepsen, 1940), and Krause (1977) has since referred that tooth to *Microcosmodon*. Unfortunately, cusp formulae cannot be determined from the broken M^1's from Dell Creek Quarry that Dorr (1952) also assigned with question to *E. powelli*. *E. powelli* and *E. tardus* may be conspecific. The systematics of both species are currently under study elsewhere (R. E. Sloan, D. W. Krause, personal communication, 1980).

Apart from Jepsen's (1930), Bown's (1979), and this record from the Willwood Formation, *E. tardus* has been recorded from the Four Mile fauna, Colorado (McKenna, 1960) and from Mutigny, France (Sloan, written communication, 1976; in Bown, 1979). *Ectypodus* [*E. lovei* (*pace* Sloan, 1966, 1981) and *Ectypodus* sp.] also occurs in the Uintan-Duchesnean deposits of Wyoming and Montana (Krishtalka and Black, 1975)—a conclusion recently strengthened by recovery of a complete P_4 *Ectypodus* from these sediments.

Oligocene multituberculates were first reported from the early Chadronian Pilgrim Creek locality, Wyoming (Sutton and Black, 1972) on the basis of a broken upper molar provisionally identified as *Parectypodus*. More recent study indicates that this tooth, along with others recovered from other Chadronian deposits in Wyoming, Nebraska and Saskatchewan document the survival of *Ectypodus lovei* and *Ectypodus* sp. into the Oligocene (Krishtalka et al., 1982).

Parectypodus Jepsen, 1940
Parectypodus sp.
(Fig. 2)

Referred specimens.—Partial dentary with I, P_4, CM 12109, 28954; broken P_4, CM 38559; isolated P^4, CM 12108.

Locality.—CM 681, Elk Creek facies, Willwood Formation, Wyoming.

Known distribution.—Wasatchian of Colorado, Wyoming, North Dakota; Sparnacian of England, France.

Description: mandible.—CM 12109 preserves part of a left dentary with a complete incisor, P_4, and the alveolar region of the molars. The coronoid process, condylar process, and posterior area of the jaw are broken away. In labial aspect, the ventral margin of the jaw is convex from the anterior end to a point below the posterior root of P_4, and is straight thereafter. The linear bulge that continues posteriorly as the anterior edge of the ascending ramus originates just posterior to the exodaenodont lobe of P_4. The mental foramen occurs near the dorsal margin of the jaw, approximately midway between the exodaenodont lobe of P_4 and incisor alveolus. The depth of the preserved parts of the masseteric and temporal fossae has been exaggerated by breakage and lateral compression of the external wall of the dentary. The dorsal surface of the dentary is smooth anterior to P_4; there is no P_3 or alveolus for that tooth.

Incisor.—The incisor is severely laterally compressed at the tip and divided into external and internal surfaces by strong dorsal and ventral ridges. A third longitudinal ridge subdivides the internal face into a narrow, flat dorsal and broader, concave ventral surface. The external surface is convex. The incisor becomes larger and more nearly ovoid posteriorly, as the ridges weaken and disappear.

P_4.—The labial profile of P_4 (L, 3.7) is high and convex anteriorly to the sixth or seventh serration, and then slopes in a straight line posteroventrally. The lower two-thirds of the anterior edge is straight whereas the remaining distance to the first serration is convex. The relative height of the first serration

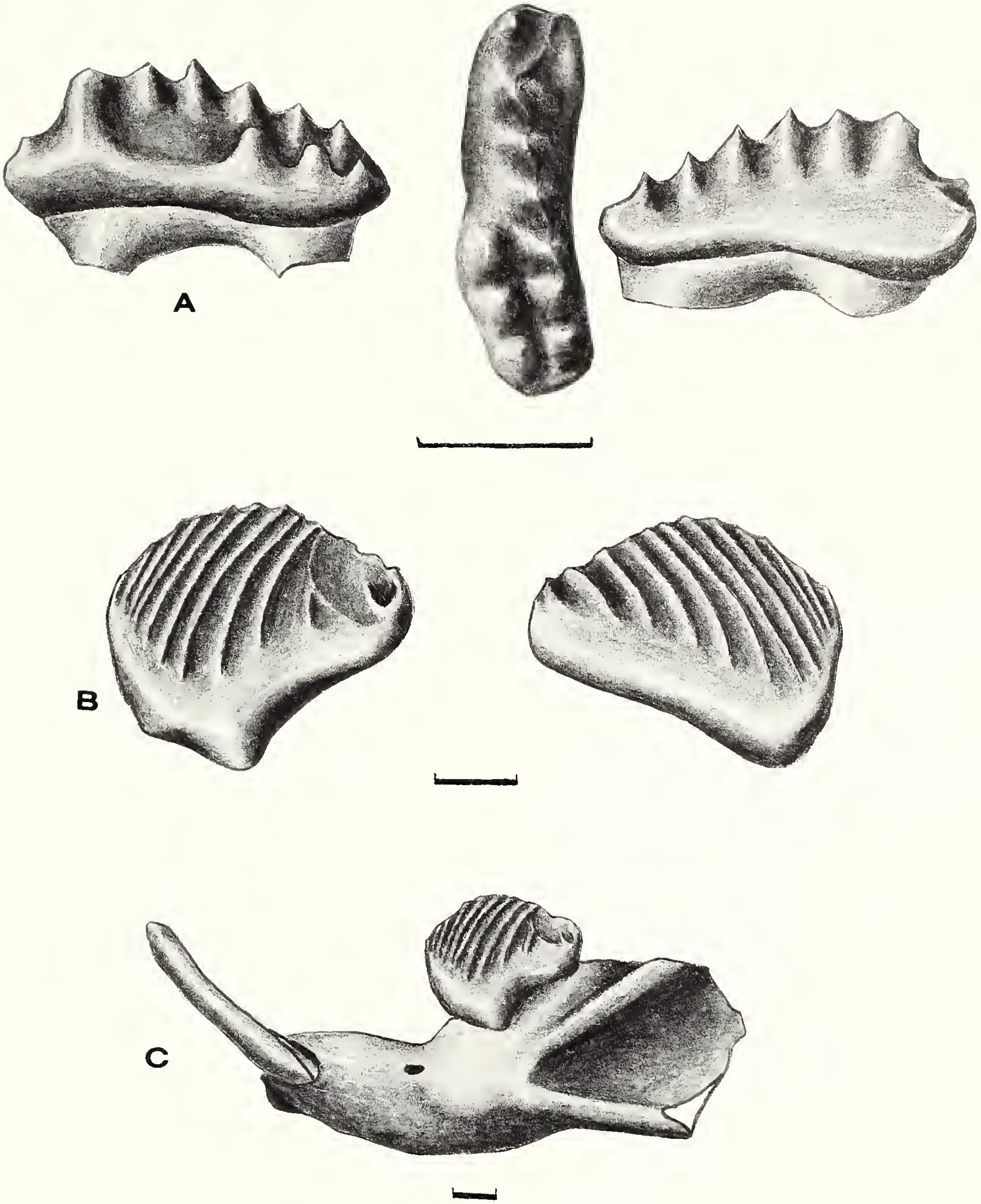

Fig. 2.—*Parectypodus* sp. A. CM 12108, left P^4; labial, occlusal and lingual views. B. CM 12109 (part), left P$_4$; labial and lingual views. C. CM 12109, left dentary with I, P$_4$; labial view. Scale indicates one mm.

is slightly less than 50% (0.46) on both blades, and there are 12 (CM 12109) or 11 (CM 28954) serrations, of which the third is highest above the line for standard length. Ridges from the first two serrations are weak and short, whereas the posterior ridges are stronger and progressively more widely spaced. The ridge from the eighth serration is longest and ends at the dorsal margin of the exodaenodont lobe. On CM 28954 the lingual ridge from the last serration runs down the posterolingual border of the blade and ends at the posterior root. Both P$_4$'s have a moderately developed posterolabial ledge and a weak, shallow anterobasal depression, which on CM 28954 leads to a faint groove on the anterior root. The latter is not exposed on CM 12109.

P^4.—CM 12108 (L, 2.0; W, 0.7) has a cusp formula of 3:6. The crown is gently arched in occlusal aspect. Its lingual margin is concave, whereas the labial border is sinuous: convex from the anterior margin to the level of the fourth medial cusp, shallowly concave between the fourth and fifth cusps, and convex from the fifth cusp to the posterior margin. In lateral view, the anterior profile of the internal crest is low and barely convex; it rises in a straight line to the fourth cusp and descends slightly to the sixth cusp. The posterior profile is short and concave. The first medial cusp is small. The remaining five are larger and subequal. The three external cusps occur opposite their lingual counterparts and increase in size from the first to the third. A tiny posterobasal cuspule occurs near the base of the posterior slope.

Remarks.—The profile of P_4 and the relative height of the first serration are *Parectypodus*-like among known neopagiaulacids (Sloan, 1966, 1981). On these criteria, as well as larger size, these two P_4's are easily distinguished from those of *E. tardus.* P^4 also resembles that of *Parectypodus* in that the anterior profile is low, the antepenultimate cusp is highest, and the posterior slope is short and concave. In size and morphology these premolars closely resemble those of a species of *Parectypodus* that Sloan (1980) has identified from the Four Mile fauna (McKenna, 1960; Sloan, 1966), the Powder River local fauna (Delson, 1971), the Golden Valley Formation (West, 1973), and the lower Willwood No Water fauna (Bown, 1979). This species, *P. childei,* is based on the type material (2 P_4's) of *Charlesmooria childei* Kühne (1969) from Abbey Wood, England, which, in my opinion, are not *Parectypodus*-like and are likewise distinct from all other P_4's assigned by Sloan to *P. childei.* The true affinities of *C. childei* as well as the systematics of the *Parectypodus* material described here and from the above North American localities are under study elsewhere (Krause, personal communication, 1980). P_4's of this species of *Parectypodus* range in length from 2.8–3.8 mm and have 9–12 serrations. P_4 of *P. simpsoni* Jepsen, 1930, the only other known Wasatchian species of *Parectypodus,* is significantly larger (4.0–4.5 mm) and has more serrations (14).

Suborder Taeniolabidoidea Sloan and Van Valen, 1965

Family Eucosmodontidae Jepsen, 1940

Neoliotomus Jepsen, 1930

Neoliotomus ultimus
(Granger and Simpson, 1928)

Referred specimen.—Fragment of a dentary with P_4 and part of I, CM 12184.

Locality.—CM 150, Elk Creek facies, Willwood Formation, Wyoming.

Known distribution.—Wasatchian of Wyoming and Colorado.

Description.—Part of the incisor is preserved and exposed in the dentary below P_4. It is highly compressed (depth, 6 mm; width, 2.1 mm) and has a band of enamel that is restricted to the lower one-half and lower one-third of the external and internal surface, respectively. In end view, the external surface of the incisor is convex and the internal one barely concave.

P_4 (L, 12.2; W, 3.6) has 13 serrations and a long low profile that is slightly higher anteriorly than posteriorly. In labial view the occlusal margin of the crown is arcuate between the top of the anterobasal concavity and the first serration, virtually straight from the first to the seventh serration, and convex from the latter to the last serration. The last four serrations are cusp-like and the posterolabial ledge is tiny. The labial and lingual ridges from each of the first 10 serrations are complete, but the eleventh ridges do not reach the base of the serration. The penultimate buccal ridge is weak; the last labial and last two lingual ridges are absent. A small, peg-like P_3 occurs below the anterobasal depression of P_4.

Remarks.—P_4 is only slightly longer than in the type of *N. ultimus* and has one less serration, whereas it is significantly smaller than P_4 of *N. conventus. N. ultimus* has also been recorded from the Sand Creek facies of the Willwood Formation (Bown, 1979), the Powder River local fauna (Delson, 1971), and the Four Mile fauna (McKenna, 1960).

CONCLUSIONS

Two neoplagiaulacids, *Ectypodus tardus* and *Parectypodus* sp., and one eucosmodontid, *Neoliotomus ultimus,* were recovered from deposits representing the Elk Creek facies of the lower Willwood Formation—a record consistent with other early Wasatchian faunas. *E. tardus* and the Tiffanian *E.*

powelli may prove to be conspecific. Although *Ectypodus* has not been found in Bridgerian faunas, its occurrence in certain late Eocene and early Oligocene ones indicates an artificially disjunct record of multituberculate evolution in the Eocene. Knowledge of the temporal extent and taxonomic diversity of Tertiary multituberculates will increase as hitherto unsampled or poorly sampled Eocene and Oligocene facies are discovered.

ACKNOWLEDGMENTS

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LITERATURE CITED

Ameghino, F. 1890. Los plagiaulacideos argentinos y sus relaciones zoologicas, geologicas y geographicas. Bol. Instituto Geographico Argentino, 9:143–201.

Bown, T. M. 1979. Geology and mammalian paleontology of the Sand Creek facies, lower Willwood Formation (Lower Eocene), Washakie County, Wyoming. Mem. Geol. Survey Wyoming, 2:1–151.

Delson, E. 1971. Fossil mammals of the early Wasatchian Powder River local fauna, Eocene of northeast Wyoming. Bull. Amer. Mus. Nat. Hist., 146:309–364.

Dorr, J. A., Jr. 1952. Early Cenozoic stratigraphy and vertebrate paleontology of the Hoback Basin, Wyoming. Bull. Geol. Soc. Amer., 63:59–94.

Granger, W., and G. G. Simpson. 1928. Multituberculates in the Wasatch Formation. Amer. Mus. Novit., 312:1–4.

Gregory, W. K., and G. G. Simpson. 1926. Cretaceous mammal skulls from Mongolia. Amer. Mus. Novit., 225:1–20.

Holtzman, R. C. 1978. Late Paleocene mammals of the Tongue River Formation, western North Dakota. North Dakota Geol. Surv. Rept. Inv., 65:1–88.

Jepsen, G. L. 1930. New vertebrate fossils from the Lower Eocene of the Bighorn Basin, Wyoming. Proc. Amer. Phil. Soc., 69:117–131.

———. 1940. Paleocene faunas of the Polecat Bench Formation, Park County, Wyoming. Proc. Amer. Phil. Soc., 83: 217–341.

Krause, D. W. 1977. Paleocene multituberculates (Mammalia) of the Roche Percee local fauna, Ravenscrag Formation, Saskatchewan, Canada. Paleontographica, Abt. A, 159:1–36.

Krishtalka, L., and C. C. Black. 1975. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 12. Description and review of late Eocene Multituberculata from Wyoming and Montana. Ann. Carnegie Mus., 45:287–297.

Krishtalka, L., R. J. Emry, J. E. Storer, and J. F. Sutton. 1982. Oligocene multituberculates: youngest known record. J. Paleont., 56:791–794.

Kühne, W. G. 1969. A multituberculate from the Eocene of the London Basin. Proc. London Geol. Soc., 1658:199–202.

Matthew, W. D., and W. Granger. 1921. New genera of Paleocene mammals. Amer. Mus. Novitates, 13:1–7.

McKenna, M. C. 1960. Fossil Mammalia from the early Wasatchian Four Mile local fauna, Eocene of northwest Colorado. Univ. Calif. Publ. Geol. Sci., 37:1–130.

Sloan, R. E. 1966. Paleontology and geology of the Badwater Creek area, central Wyoming. Part 2. The Badwater multituberculate. Ann. Carnegie Mus., 38:309–315.

———. 1979. Multituberculata. Pp. 492–498, *in* Encyclopedia of Paleontology (R. W. Fairbridge and D. Jablonski, eds.), Dowden, Hutchinson and Ross, Stroudsberg, Pennsylvania.

———. 1981. Systematics of Paleocene multituberculates from the San Juan Basin, New Mexico. Pp. 127–160, *in* Advances in San Juan Basin Paleontology (S. G. Lucas, J. K. Rigby and B. S. Kues, eds.), University of New Mexico Press, Albuquerque, New Mexico.

Sloan, R. E., and L. Van Valen. 1965. Cretaceous mammals from Montana. Science, 148:220–227.

Sutton, J. F., and C. C. Black. 1972. Oligocene and Miocene deposits of Jackson Hole, Wyoming. Field Conf. Guidebook On Tertiary Biostratrigraphy of southern and western Wyoming. Pub. Univ. Colorado Mus., pp. 73–79.

West, R. M. 1973. New records of fossil mammals from the early Eocene Golden Valley Formation of North Dakota. J. Mamm., 54:749–750.

Address: Section of Vertebrate Fossils, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213.

Note Added in Proof

Since this paper was reviewed and accepted for publication (1980), Krause (1982) has published a systematic review of North American Wasatchian multituberculates. In agreement with views presented here, Krause assigned *Charlesmooria childei* to *Ectypodus* (rather than *Parectypodus,* contra Sloan, 1981), and included the CM material of *Parectypodus* sp. (except CM 12108) in a new species, *P. lunatus*; CM 12108, a P^4, was transferred to *E. tardus.* Also since 1980, Stucky and Krishtalka (1982) have recorded *Ectypodus* sp. cf. *E. childei* from Lostcabinian localities in the Wind River Formation, northeastern Wind River Basin.

Krause, D. W. 1982. Multituberculates from the Wasatchian Land-Mammal Age, early Eocene, of western North America. J. Paleont., 56:271–294.

Stucky, R. K., and L. Krishtalka. 1982. Revision of the Wind River faunas, early Eocene of central Wyoming. Part 1. Introduction and Multituberculata. Ann. Carnegie Mus., 51: 39–56.

INSECTIVORA, SCIURIDAE, AND CRICETIDAE FROM THE EARLY MIOCENE ROSEBUD FORMATION IN SOUTH DAKOTA

James E. Martin and Morton Green

ABSTRACT

The small mammals in the Black Bear Quarry II local fauna from the Rosebud Formation increases the diversity of the early Hemingfordian fauna. These forms both include primitive remnants of Oligocene stocks and herald the late Hemingfordian and Barstovian faunas. The latest known occurrence of a geolabidid(?) is noted, a new hedgehog, *Hibbarderix obfuscatus,* is described, and more Hemingfordian cricetids are included. The fauna also adds to our knowledge environmentally as it appears to represent a non-riparian assemblage.

INTRODUCTION

The insectivores and rodents from the Black Bear Quarry II locality (SDSM V671) in the Rosebud Formation are described with some exceptions. The Talpidae (with one exception) are being studied by J. H. Hutchison, the Eomyidae by M. A. Jones, and the Geomyoidea by Morton Green and P. R. Bjork. The Lagomorpha have been reported by Green (1972), the Didelphidae by Green and Martin (1976) and the Zapodidae by Green (1977*a*). The described specimens are mostly isolated teeth with few fragments of jaws. This poor preservation introduces difficulty in some generic and specific assignments. We have, therefore, been conservative in naming these distinctive but isolated elements.

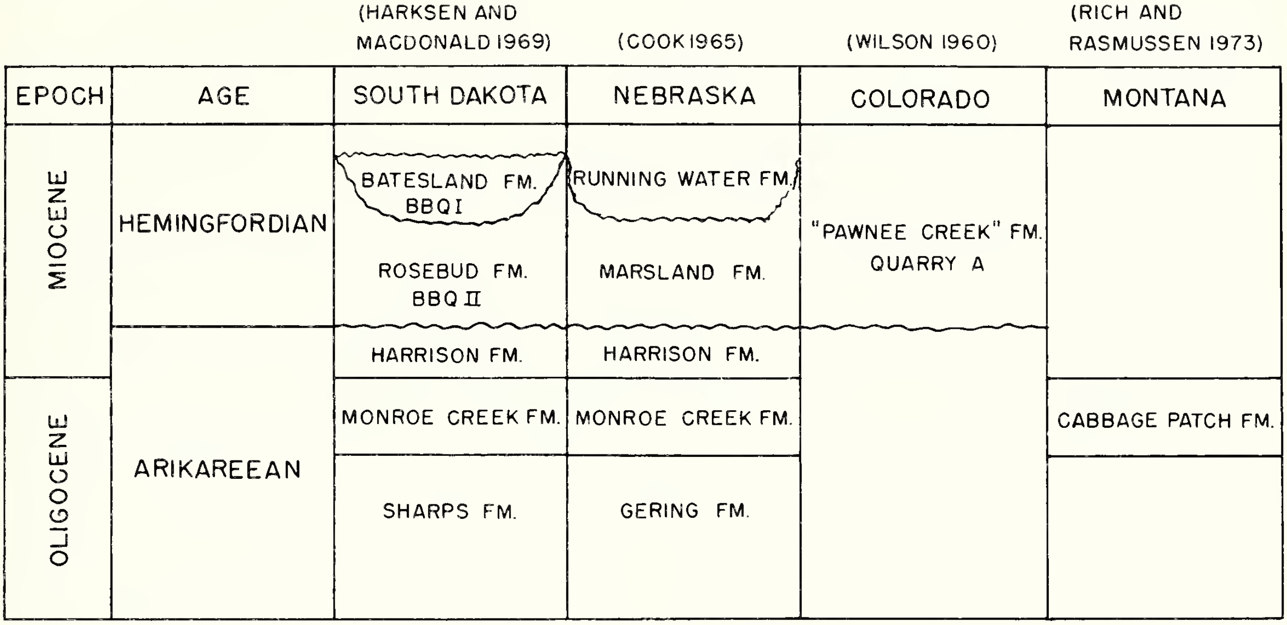
The collecting techniques and description of this locality have already been described by one of us (Green, 1972). Acronyms and abbreviations used are: SDSM, Museum of Geology, South Dakota School of Mines and Technology; BBQ II, Black Bear Quarry II (early Hemingfordian); AP, greatest anteroposterior measurement; Tr, greatest transverse measurement; N, number of specimens; $\bar{X}$, mean; SD, standard deviation; C.V., coefficient of variation. Measurements are in millimeters. Our thanks to P. R. Bjork and R. W. Wilson for suggestions and criticisms. The drawings were made by Merton C. Bowman. John E. Storer and Larry D. Martin reviewed the manuscript.

RELATIONSHIP OF FAUNA

This is another contribution in an overall investigation of the Miocene sediments in southwestern South Dakota. The Black Bear Quarry II fauna fits stratigraphically between two previously described Miocene faunas in South Dakota (Fig. 1). The Monroe Creek Formation occurs below the Rosebud Formation, whereas it is overlain by the Batesland Formation. Faunas have been described from these two units by L. J. Macdonald (1972) and J. E. Martin (1976), respectively. One of the four Batesland localities (Black Bear Quarry I, SDSM V672) is found about 30 m above the Rosebud locality. It is not very surprising that, when the faunas from these two formations are compared, the fauna from BBQ II is more like that of Black Bear Quarry I. BBQ II also has genera in common with other faunas described from elsewhere on the Great Plains, especially the Martin Canyon, Quarry A fauna (Wilson, 1960). Stratigraphic relationships of some mid-Tertiary formations are illustrated in Fig. 1.

BIOSTRATIGRAPHY OF SMALL MAMMALS OF THE SOUTHWESTERN SOUTH DAKOTA MID-TERTIARY

The occurrence of a thick section of Oligocene and Miocene sediments in southwestern South Dakota provides an opportunity to study a faunal succession in a limited geographic area. As can be noted in Fig. 1, the composite section extends from the Sharps Formation through the Batesland For-



		(HARKSEN AND MACDONALD 1969)	(COOK 1965)	(WILSON 1960)	(RICH AND RASMUSSEN 1973)
EPOCH	AGE	SOUTH DAKOTA	NEBRASKA	COLORADO	MONTANA
MIOCENE	HEMINGFORDIAN	BATESLAND FM. BBQ I	RUNNING WATER FM.	"PAWNEE CREEK" FM. QUARRY A	
		ROSEBUD FM. BBQ II	MARSLAND FM.		
	ARIKAREEAN	HARRISON FM.	HARRISON FM.		
OLIGOCENE		MONROE CREEK FM.	MONROE CREEK FM.		CABBAGE PATCH FM.
		SHARPS FM.	GERING FM.		

Fig. 1.—Relationships of some Mid-Tertiary formations on the Great Plains.

mation. With the exception of the Harrison Formation, faunas from these units have been described by J. R. Macdonald (1963, 1970), L. J. Macdonald (1972), Green (1972, 1977*a*), Hutchison (1972), J. E. Martin (1976), and Green and Martin (1976). A small collection of micromammals from the Harrison Formation has been made by us, but has not been completely evaluated. Some elements are included in Table 1, but it must be remembered that the fauna is not as well known as the others. This table gives some idea of the biostratigraphic relationships in a limited geographic area. As more information becomes available, this list can be expanded into other regions and faunal elements revised.

From Table 1 it can be noted that the most primitive mammal of the faunas, *Peratherium*, ranges throughout the Oligocene-Miocene section in South Dakota, and the Batesland Formation represents its highest known occurrence. Of the insectivores, the range of the Geolabididae is extended into the early Hemingfordian. *Antesorex, Hibbarderix*, and *Wilsonosorex* are restricted to the Hemingfordian, but representatives probably will be found lower in the section. *Parvericius, Brachyerix*, and *Scalopoides* appear in the Monroe Creek Formation and range throughout. *Heterosorex* also seems continuous, but has not yet been identified from the Rosebud sediments. *Proscalops* evolved into *Mesoscalops* in the Hemingfordian.

The lagomorphs and their relationships within the region have been discussed by Green (1972) and Martin (1976). Most of the more primitive described rodents such as *Prosciurus*, and some aplodontids and mylagaulids appear restricted to the Arikareean. *Promylagaulus* and *Mylagaulodon* have been found in the Rosebud Formation (J. R. Macdonald, 1970), but were not found at BBQ II. Fragmentary aplodontoid specimens are known from the Batesland Formation, but have not yet been described. *Leidymys, Paciculus, Tamias*, and primitive eomyids retaining *Adjidaumo* characteristics appear to exist throughout this span. The Batesland Formation represents the last occurrence of the two cricetid genera in this area. The advanced eomyids, such as *Pseudotheridomys*, appear in the Hemingfordian. The larger squirrels and *Plesiosminthus* appear in the Monroe Creek Formation. The only beaver known from thus far sampled Hemingfordian deposits is an undescribed new genus; no beavers were recovered from BBQ II. Of course, with continued investigation, these first and last occurrences are subject to change.

Although the evidence is not complete, considerable modernization of the small mammal faunas occurred during deposition of the Monroe Creek Formation. Many first appearances including some migrants from Eurasia are found together with primitive forms. However, when the small mammals from the Harrison Formation are described, they will probably emphasize the Arikareean-Hemingfordian boundary as a time of more extreme change. This is illustrated in Table 1 where it can be seen that by the time of Rosebud deposition, many new genera occur.

SYSTEMATIC PALEONTOLOGY

Order Insectivora Bowdich, 1821
Family Erinaceidae Fischer von Waldheim, 1817
Family Geolabididae McKenna, 1960
Geolabididae?

Genus and species indeterminate

Fig. 2

Material.—SDSM 8702, right $M^{1 \text{ or } 2}$; SDSM 8667, seven $M^{1 \text{ or } 2}$; SDSM 8668, five M^3.

Description.—These molars resemble those of other geolabidids in possessing a strong stylar shelf; a very prominent parastyle; very narrow, anteriorly directed trigon; absence of conules; and diminutive hypocone, well separated from the trigon. The paracone and metacone are closely appressed, but not quite to the degree exhibited by other geolabidids. The stylar shelf is not indented between these two cusps. The latter character is unlike the condition in most geolabidids as is the lack of a cingulum anterior to the protocone. Another difference from later occurring species of *Centetodon* (Lillegraven et al., 1981) is the presence of fused lingual roots similar to *Ankylodon.* Crests extend from the three roots to the center of the tooth as is typical of erinaceids and geolabidids. Most molars have no ridge between the metacone and protocone (Fig. 2), but two specimens possess this ridge as in other described geolabidids. The M^3's differ slightly from the anterior molars. They do not appear to be as elongate transversely and are smaller (Table 2).

Discussion.—With some modifications, these teeth retain the very high delicate cusps characteristic of the earlier geolabidids. An M^2 referred to *Geolabis* sp. from the Arikareean Monroe Creek Formation (L. J. Macdonald, 1972:17) and a mandible with M_2–M_3 from the early Arikareean Middlebranch l.f. (Voorhies, 1973:5) are stratigraphically the youngest geolabidids heretofore recorded. Unfortunately some of the important characters of the M^2 were not preserved. The nature of the hypocone and of the internal roots cannot be precisely determined. It does appear that a hypocone was present, however, and possibly an anterior cingulum. The roots were probably divided. Therefore, on the Rosebud specimens the two lingual roots, the anterior cingulum, and external notching of the stylar shelf are absent. The paracone and metacone becoming slightly more separated are unique features. These characters are distinct enough to justify a new genus, but the lack of more definitive material, especially lower teeth, prevents us from proposing a name at this time.

These characters pose some questions as to the derivation of this species from the Oligocene geolabidid stock. Perhaps by early Hemingfordian a hedgehog had evolved from the Geolabididae possessing these characters. Alternatively, these teeth may be those of a unique insectivore and not a member of the Geolabididae. The fused roots tend to support this alternative, perhaps indicating a hedgehog paralleling the structure of earlier geolabidids. Other specimens must be found before either hypothesis can be substantiated. All that can now be stated with certainty is that these teeth are morphologically most similar to species of Geolabididae.

Family Erinaceidae, Fischer von Waldheim, 1817
Subfamily Erinaceinae Gill, 1872

Hibbarderix, new genus
Hibbarderix obfuscatus, new species

Figs. 3–8

Etymology.—For C. W. Hibbard, in recognition of his pioneering efforts in screen washing, the method used in the recovery of these specimens and for his many other contributions to the science of vertebrate paleontology; plus L. *ericius,* hedgehog: L. *ob,* toward; L. *fuscare,* to darken.

Type.—SDSM 8703, right M^1; AP 1.87, Tr 2.40.

Hypodigm.—SDSM 8673, three P^3; SDSM 8674, SDSM 8701, P^4; SDSM 8675, nine M^1; SDSM 8676, fifteen M^2 (two broken); SDSM 8677, two M^3; SDSM 8669, fragment of left mandible with alveoli for I, antemolar 1, P_2, and P_3, P_4–M_1 (broken); SDSM 8670, eleven M_1; SDSM 8671, eleven M_2; SDSM 8672, eleven small M_2 (questionably referred).

Diagnosis.—M^1–M^2: small with delicate cusps; molars wider transversely than long; prominent metaconule; no paraconule; no external notching of the wide stylar shelf; robust hypocone with cingulum surrounding the base resulting in a quadrate tooth outline of M^1. M_1–M_2: anteroposteriorly compressed trigonid with high slender cusps; no hypoconulid; deeply incised paralophid and protolophid on unworn M_1.

Description.—The upper molars are most diagnostic for this genus. The lower teeth are conservative and difficult to use in a generic differentiation. This was noted by Rich and Rasmussen (1973) when they regarded compression of the trigonid as important in separation of some of their species. With *Hibbarderix* it is the upper teeth which are most distinctive and significant. Both upper and lower molars possess interradicular crests.

P^3 is four-cusped with the paracone dominant. The parastyle is well developed and the metastyle is a prominent ridge directed posteriorly from the paracone. The protocone is normally a distinct conical cusp. On P^4 the paracone and metastyle form an external blade. A parastyle may be present or a small cingulum takes its place at the base of the paracone. The protocone and hypocone appear as cuspules on the anterior edge of the large, internal shelf. M^1 possesses a large external shelf (stylar shelf). There is a distinct parastyle, whereas the metastyle is connected to the metacone by a long, blade-like ridge. Most distinctive is the metaconule; the paraconule is absent. The protocone is a pointed, V-shaped cusp connected via a single crest to the conical hypocone. The anterior arm or crest of the protocone extends to the base of the paracone. There appears to be some tendency for anterior intersection but it never reaches the parastyle. The tooth has a quadrate shape as a result of the well developed anterior and posterior cingula. M^2 is similar to M^1 except that it is more triangular in outline, and the external shelf is smaller, especially the metastyle blade. The small M^3 specimens possess three cusps in a transverse line similar to M^3 of *Parvericius.*

P_4 has a prominent paraconid and protoconid, but the metaconid and talonid are reduced. A mental foramen is present beneath this double rooted tooth. The trigonid of the M_1 is anteroposteriorly compressed, but a deep extensive trigonid basin is present due to deep V-shaped cuts in the paralophid and protolophid. The incision of the paralophid is acute in unworn specimens. The cutting edge of the paralophid blade from the incision to the paracone has an undulatory outline from a labial view. The talonid basin is very deep and wide. A high pointed entoconid dominates the V-shaped hypoconid. The external cingulum is usually weak. M_2 is similar to M_1, but the talonid appears shortened relative to the trigonid. Measurements, SDSM 8669: P_4, AP 1.35; Tr 1.00. M_1, AP 2.30; Tr 1.35. Depth of jaw below posterior root of P_4, 2.6.

Table 1.—*Small mammals from the South Dakota Mid-Tertiary.*[1]

	Formation				
Taxa	Sharps 117.4 m	Monroe Crk. 27.4 m	Harrison 39.0	Rosebud 67.0 m	Batesland 14.0 m
Marsupialia:					
Peratherium	—	—	—	—	—
Insectivora:					
Geolabididae	- - -	—	- - -	—	
Plesiosorex					—
Ocajila	—				
Amphechinus		—			
Hibbarderix				—	—
Parvericius		—	- - -	—	
Brachyerix		—			
Domnina	—				
Heterosorex	—	—	- - -	- - -	—
Wilsonosorex				—	—
Antesorex				—	—
Proscalops	—	—			
Mesoscalops				—	—
Quadrodens	—				
Mystipterus					—
Scalopoides		—	- - -	—	—
?Uropsilinae				—	
Primates:					
Ekgmowechashala	—				
Lagomorpha:					
Gripholagomys		—	- - -	—	—
Palaeolagus	—	—			
Archaeolagus		—	- - -	—	
Hypolagus					—
?*Megalagus*	—				
Rodentia:					
Prosciurus	—				
Downsimus	—				
Allomys	—	—			
Meniscomys	—				
Niglarodon	—				
Promylagaulus		—	- - -	—	
Mylagaulodon				—	
Protosciurus		—			
Tamias	—	- - -	- - -	—	—
Miospermophilus		—	- - -	—	—
Protospermophilus		—	- - -	- - -	—
Palaeocastor	—	—			
Capatanka	—	—			
Capacikala	—	- - -	—		
Castoridae (new genus)					—
Eutypomys	—	—			
Eomyidae (primitive)		—	- - -	- - -	—
Pseudotheridomys				—	—
Eomyidae (large)				—	—
Geomyoidea	—	—	—	—	—
Leidymys	—	—	- - -	—	—
Paciculus	—	—			—
Cricetidae (small)				—	? —
Plesiosminthus		—	—	—	—

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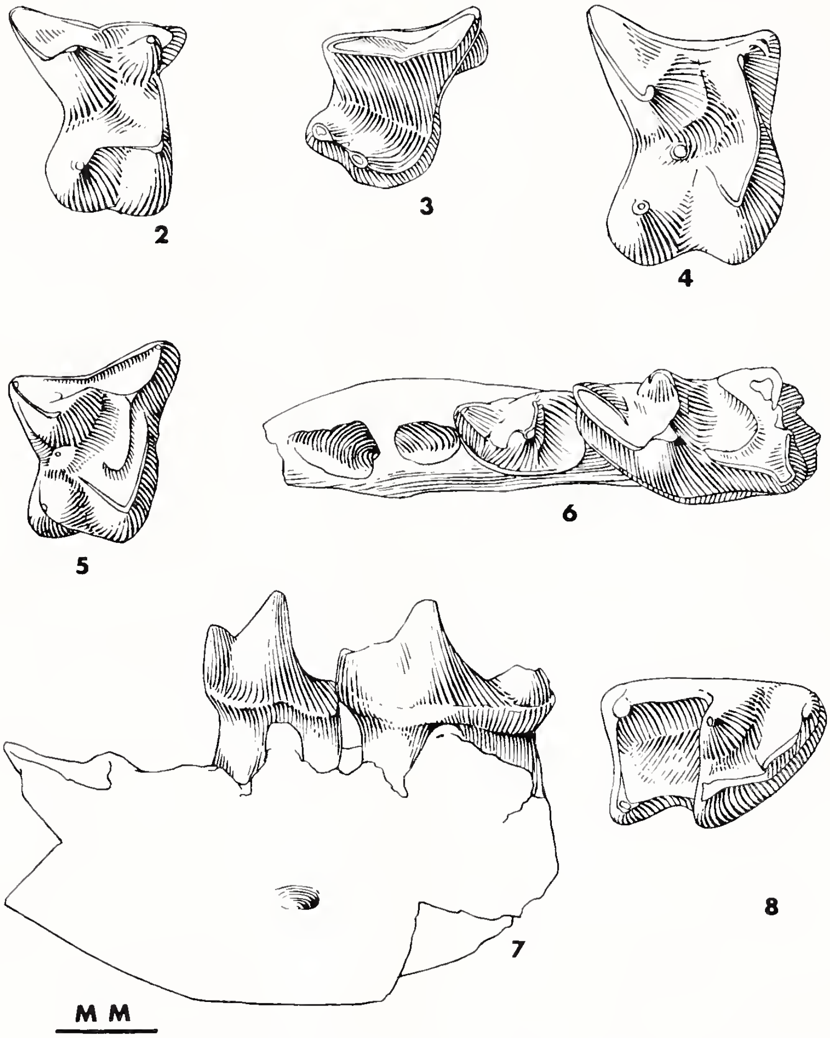
[1] Solid lines indicate presence in, not distribution, within formation. Dashed line indicates presumed presence. Thickness given in meters.

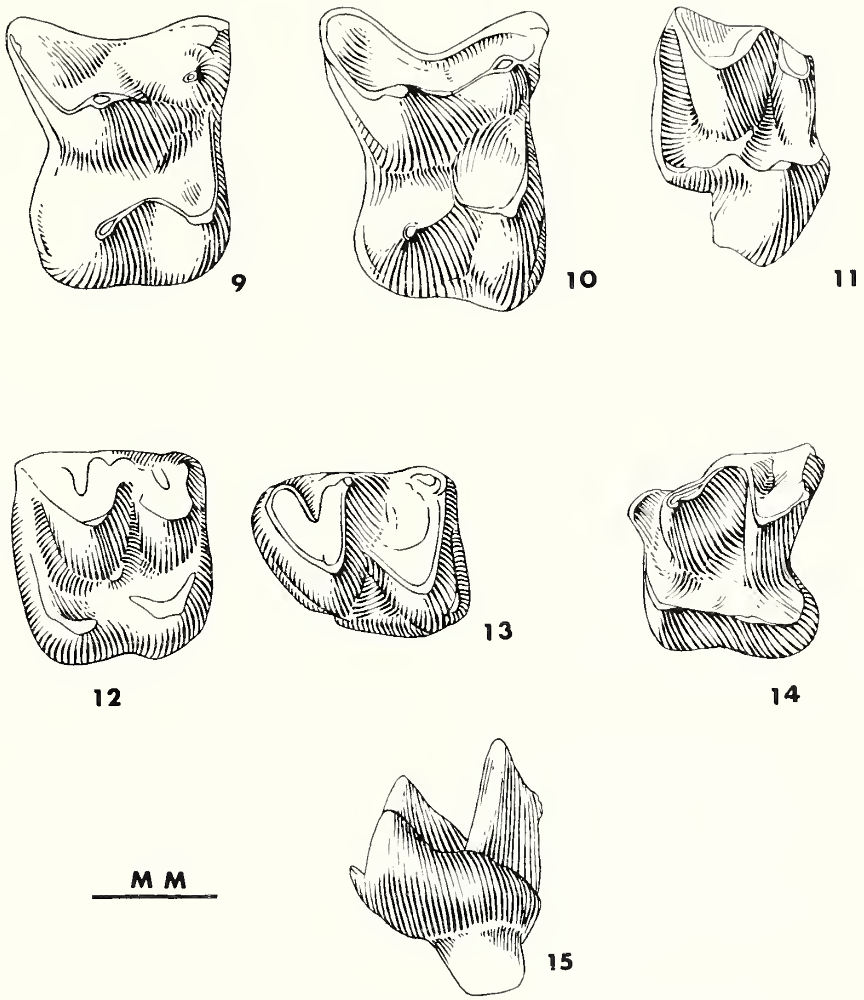
Discussion.—Morphologically, *Hibbarderix* is



Figs. 2–8.—2) Geolabididae?, SDSM 8702, right M^1 or M^2. 3) *Hibbarderix obfuscatus*, SDSM 8701, right P^4. 4) *Hibbarderix obfuscatus*, SDSM 8703, right M^1, holotype. 5) *Hibbarderix obfuscatus*, SDSM 8676, right M^2. 6) *Hibbarderix obfuscatus*, SDSM 8669, crown view of left lower teeth (P_4–M_1). 7) *Hibbarderix obfuscatus*, SDSM 8669, lateral view of left lower jaw. 8) *Hibbarderix obfuscatus*, SDSM 8670, right M_1. Scale = 1 mm.

most similar to *Stenoechinus* Rich and Rasmussen, 1973. *Hibbarderix* exhibits the anteroposteriorly-compressed trigonid of the lower molars, delicately constructed cusps, and greater width of M^1 compared to its length. It can be differentiated from this genus by: the presence of a metaconule on M^1–M^2, no indentation of external shelf on M^1, more quadrate tooth outline of M^1 due to a better developed posterior cingulum, a deep and acutely notched paralophid on M_1, and a somewhat more compressed trigonid. The degree of this last character varies somewhat, but overall it appears valid.

Hibbarderix can be distinguished from all other hedgehogs on the basis of size and the presence of a metaconule on M^1 and M^2. The only genera of hedgehogs described in the North American Hemingfordian and Barstovian as possessing a metaconule are *Meterix, Plesiosorex,* and *Lantanotherium.* Recently, Green (1977*b*) placed *Meterix* in the synonymy of *Plesiosorex.* Compared with *Plesiosorex, Hibbarderix* is much smaller and more delicate. The upper molars of *Hibbarderix* are distinctive in possession of a wide external shelf, no medial indentation of the shelf, lack of cuspate styles, and a square tooth outline of M^1. The lower molars of *Hibbarderix* do not possess a hypoconulid, and the position



Figs. 9–15.—9) cf. *Parvericius* species, SDSM 8678, right M^1. 10) cf. *Parvericius* species, SDSM 8704, right M^1. 11) *Wilsonosorex* species, SDSM 8681, right M^1. 12) *Wilsonosorex* species, SDSM 8681, right M^1. 13) *Wilsonosorex* species 8681, left M_1. 14) Uropsilinae?, SDSM 8700, left M^1, crown view. 15) Uropsilinae?, SDSM 8700, left M^1, lingual view. Scale = 1 mm.

of the mental foramen differs from the American, but not European species. *Lantanotherium* is unique due to lack of a distinct paraconid on M_1, no stylar shelf on the upper molars, and the greater development of M^2–M^3.

Hibbarderix, like *Stenoechinus*, differs from most Old World erinaceines by a greater transverse width of M^1 compared with its length, combined with the compressed M_1 trigonid. Of the Miocene genera, *Amphechinus* and *Mioechinus* differ in having only a faint metaconule and external notching of M^1.

Hibbarderix provides another indication of the diversity of early Miocene hedgehogs. The metaconule on M^1–M^2 could suggest a primitive member of this group, indicating survival of a primitive line, or perhaps the conule is a newly acquired character. The former suggestion might be the more likely because the Arikareean genus *Ocajila* Macdonald from the Cabbage Patch beds of Montana, possesses metaconules (Rasmussen, in preparation). However, the Montana genus differs from *Hibbarderix* in possessing both a metaconule and paraconule on M^1–M^2, a well formed paracone and hypocone on P^4, a triangular M^3, and a reduced paraconid on M_1–M_2. More species of late Arikareean and early Hemingfordian erinaceines must be found before the phylogenetic position of *Hibbarderix* can be substantiated.

In this regard, there is another occurrence of this genus. While the publication concerning the small

Table 2.—*Geolabididae? Genus and species indeterminate.*

Measurement	N	Observed range	Mean	SD	C.V.
		SDSM 8667 M^1 or M^2			
AP	4	1.62–1.80	1.76	±0.09	5.11
Tr	7	2.01–2.38	2.20	±0.13	5.91
		SDSM 8668 M^3			
AP	4	1.05–1.39	1.25	±0.14	11.20
Tr	4	1.50–1.78	1.70	±0.13	7.65

Table 4.—*cf.* Parvericius *species.*

Museum no., tooth	Measurement	N	Observed range	Mean	SD	C.V.
SDSM 8679, M^1	AP	3	2.00–2.40	2.24	±0.20	8.93
	Tr	4	2.85–3.40	3.08	±0.27	8.77
SDSM 8679, M^2	AP	1		1.91		
	Tr	1		2.70		
SDSM 8680, M_1	AP	2	2.40–2.85	2.63	±0.32	12.17
	Tr	2	1.60–1.75	1.68	±0.11	6.55

mammals from the Batesland Formation (Martin, 1976) was in press, Martin had the opportunity to study the types of *Parvericius montanus* Koerner and *Stenoechinus tantalus* Rich and Rasmussen. This examination showed that the Batesland species of hedgehog was not referable to *Parvericius,* but to *Hibbarderix.* The Batesland species is close to *H. obfuscatus,* but appears to have more massive cusps. Also, if the P^4 from Flint Hill North belongs to *Hibbarderix,* it has a better developed parastyle and hypocone than *H. obfuscatus.* This tooth appears somewhat large for the other erinaceine teeth, but is much smaller than those of *Plesiosorex coloradensis* from the same quarry. Perhaps this tooth represents a third hedgehog occurring in the Batesland Formation. Storer (1975), described *Parvericius* from the Wood Mountain fauna. It is an erinaceid with a metaconule. This specimen may be referable to *Hibbarderix,* which, if it is, extends the range of the genus into the Barstovian.

Table 3.—Hibbarderix obfuscatus.

Museum no., tooth	Measurement	N	Observed range	Mean	SD	C.V.
SDSM 8670, M_1	AP	9	2.10–2.30	2.19	±0.09	4.11
	Tr	9	1.20–1.50	1.38	±0.10	7.25
SDSM 8671, M_2	AP	9	1.75–2.09	1.91	±0.13	6.81
	Tr	10	1.09–1.38	1.21	±0.11	9.09
SDSM 8672, M_2	AP	10	1.45–1.62	1.56	±0.05	3.21
	Tr	8	0.99–1.20	1.06	±0.08	7.55
SDSM 8673, P^3	AP	3	1.00–1.15	1.05	±0.09	8.57
	Tr	3	1.12–1.35	1.23	±0.12	9.76
SDSM 8674, P^4	AP	1		1.85		
	Tr	1		1.89		
SDSM 8675, M^1	AP	8	1.89–2.05	1.96	±0.06	3.06
	Tr	8	2.10–2.65	2.42	±0.18	7.44
SDSM 8676, M^2	AP	12	1.49–1.75	1.61	±0.09	5.59
	Tr	12	1.85–2.20	2.04	±0.12	5.88
SDSM 8677, M^3	AP	2	1.15–1.18	1.17	±0.02	1.71
	Tr	2	0.58–0.65	0.62	±0.05	8.06

cf. *Parvericius* species
Figs. 9, 10

Material.—SDSM 8678, M^1; SDSM 8679, two M^1, one M^2; SDSM 8704, right M^1; SDSM 8680, one M_1, one M_2.

Discussion.—These teeth resemble those described by Koerner (1940) and Rich and Rasmussen (1973) for *Parvericius montanus* Koerner. They are larger (Tables 3–4), more robust, and do not possess metaconules as does *Hibbarderix,* the other erinaceine from the locality. The upper molars have a wide external shelf, which possesses a distinctive notch between the paracone and metacone. An external cingulum is present. The trigon is narrower than that of *P. montanus,* and the metaloph is poorly developed. On SDSM 8678, it does not reach to the base of the metacone, but only half the distance from the protocone to the metacone. At this point, it joins a crest originating from the hypocone. This results in a posteriorly sloping plane from the trigon basin to the posterior cingulum. The anterior crest of the protocone runs toward the parastyle, rather than the paracone. The hypocone is well developed on the M^2, and the internal roots are fused on the M^1 and M^2. The two lower molars are similar to the descriptions given for those of *P. montanus* except for the talonid of the M_1 which appears to be anteroposteriorly compressed. Interradicular crests are present between the roots of the upper molars.

Table 5.—Wilsonosorex *species (SDSM 8681).*

	Measurements	
Tooth	AP	Tr
M^1		
a	broken	2.40
b	1.91	2.25
M_1	2.15	1.8

The large robust nature of the teeth and the prominent hypocone of M^2 point to an affinity with *Parvericius.* However, the narrow trigon, delicate metaloph, and indented stylar shelf are unlike *P. montanus.* Probably another species of *Parvericius* is represented, but we do not have enough material to name the species.

Comments on the erinaceines.—The genera occurring in the Arikareean Cabbage Patch beds of Montana are: *Stenoechinus, Amphechinus, Parvericius,* and one genus of undetermined affiliation. Although *Amphechinus* is known in South Dakota from the Monroe Creek Wounded Knee fauna, it is absent in the BBQ II collection. *Parvericius* is common to both states, but *Stenoechinus* is absent in South Dakota. *Hibbarderix,* so far, is known only from BBQ II, the Batesland Formation and possibly the Wood Mountain Formation.

Family Soricidae Gray, 1821
Subfamily Heterosoricinae Viret and Zapfe, 1951
Wilsonosorex J. E. Martin, 1978

Wilsonosorex **species**
Figs. 11–13

Material.—SDSM 8681, two right M^1 and one right M_1.

Description.—One upper molar is worn and on the other the protocone and hypocone are broken. Even with this poor preservation, some characters are obvious. For instance, the mesostyle is well divided even with wear, a quadrate shape is apparent, and there are peaks of enamel in the metaconule and paraconule positions. These characters suggest affinities with *Wilsonosorex* from the Batesland Formation and from Quarry A in Colorado (Martin, 1978). However, the conules are not separated by distinct valleys from the protocone, and it cannot be determined whether the paraconule is doubled as it is in the Batesland and Colorado species. It is larger, higher cusped, and less quadrate than *W. bateslandensis.* It is most similar to *W. conulatus* from Quarry A, but differs in less anteroposterior compression of the cusps as well as the less distinct conule mentioned above.

M_1 is very robust with a high trigonid and shallow trigonid valley. The paraconid is a ridge, rather than a distinct cusp. The talonid is broad, and the hypoconid is V-shaped. The hypolophid is confluent with the entoconid, and a cingulum surrounds all but the inner side.

Discussion.—M_1 is unlike those lower molars referred to either *W. bateslandensis* or *W. conulatus* on the bases of large size, robust nature, and high trigonid. These characters might indicate that M_1 represents a different heterosoricine genus than the upper teeth. However, until more and better specimens are obtained, it is uncertain whether these teeth represent a generic unit or are mixed. The upper teeth do resemble most closely species from Colorado and the Batesland Formation. They might represent a third species of the genus.

The Hemingfordian appears to reflect a great heterosoricine diversity. *Heterosorex* and *Wilsonosorex* are now known and perhaps *Dinosorex* Engesser can be differentiated from *Heterosorex. Dinosorex* has been diagnosed in Europe (Engesser, 1972, 1975) as exhibiting a divided masseteric fossa, the posterior arm of the hypoconid (hypolophid) confluent with the entoconid, a quadrate shaped P^4, divided mesostyle, and well developed internal cusps on the upper molars. From the Batesland Formation, both an M_1 with a confluent entoconid and one without exist. The only upper tooth appears to be *Heterosorex.* In the better sample from Quarry A (Wilson, 1960), however, only lowers with confluent entoconids are known, and the masseteric fossae are divided as in *Dinosorex.* The uppers, on the other hand, do not have a divided mesostyle or well formed inner cusps as might be expected if they were *Dinosorex.* The P^4 is somewhat quadrate, but not to the degree illustrated by Engesser. At Quarry A it appears there is a mixing of diagnostic characters. This might only indicate that the European diagnoses cannot be used in North America, but more information from the Hemingfordian is required.

Subfamily Soricinae Murray, 1866

Antesorex **species cf.** ***A. compressus*** (Wilson)

Material.—SDSM 8682, fragment of right mandible with broken M_1, complete M_2, and broken M_3; SDSM 8683, fragment of right mandible with M_2–M_3.

Discussion.—These molars compare favorably with those of *A. compressus* from Quarry A (Wilson, 1960) and *Antesorex* sp. from the Batesland Formation (Martin, 1976). The primary differences from the type of *A. compressus* are the slightly larger robust trigonids and shallower talonid basins. Unfortunately, the talonid is worn or broken in M_3 of both specimens.

Although these teeth do not appear quite so delicate as those from Quarry A and the Batesland

Table 6.—Antesorex *species cf.* A. compressus.

Tooth	Measurements AP	Tr
	SDSM 8682	
M_1	broken	0.90
M_2	1.35	0.80
M_3	0.91	0.40
	SDSM 8683	
M_2	1.21	0.90
M_3	1.00	0.40

Formation, they are additional evidence showing the faunal similarities of the three.

Family Talpidae Gray, 1825
Subfamily Uropsilinae?, Dobson, 1883
Figs. 14, 15

Description.—SDSM 8700, a left M^1. On this unusual tooth the paracone and metacone are extremely high. The metastyle is broken off; the mesostyle is rounded and undivided. The paracone is a posterobuccally directed blade lacking an anterior projection to the parastyle. Thus the ectoloph does not form a complete W as the anterior arm of the paracone is absent. The parastyle is very low on the tooth, below the paracone. The metaconule is more a shelf-like extension of the posterad slope of the protocone than a cusp. This metaconule flange turns buccally and wraps around the lingually projecting base of the metacone. An enamel ridge caps the protocone and descends to the metaconule where it broadens into a cingulum that defines the rim of the flange. This is the only cingulum on this tooth. A strong posterior broadly open, V-shaped embayment is present. There is a single internal root which interestingly enough, has a faint crest, which extends to a bulge in the middle of the tooth. Another crest originates from the metaconal root but fades just posterior to the central bulge. These characters indicate the presence of still another new genus of insectivore in the BBQ II fauna. AP, 2.01; Tr 2.15.

Discussion.—This strange upper molar resembles soricid molars in its high sharp cusps and posterior extension of the inner tooth shelf. It resembles the M^1 of the desmanine talpid *Asthenoscaptor* Hutchison (1974) and the uropsilines in its deep posterior embayment, deeply indented but undivided mesostyle, and absence of a paracrista. It is unlike *Asthenoscaptor* and the Uropsilinae in the cusp height and the paraconule is more prominent on the former than in SDSM 8700. The parastyle is more pronounced as is the posterior extension of the cingulum. The latter character is so advanced as to remind one of *Sorex,* but no true hypocone exists, so we regard it as a parallel structure.

Although this species is represented by only a single tooth, it displays many of the salient features of the insectivore. Fortunately, the specimen is an unworn M^1; the morphology of this tooth has been often used in differentiating the Insectivora. Therefore, we have a solid basis for believing that we are dealing with a new form. Exactly to which talpid group it belongs is a different matter. The indentation of the posterior margin of the M^1 was cited by Hutchison (1968:14) as diagnostic of the Uropsilinae. However, in 1974 with the description of *Asthenoscaptor,* the same author noted that the Desmaninae may show the posterior enlargement of the metaconular flange with subsequent concavity between it and the ectoloph. It is possible, therefore, that the Rosebud specimen is a representative of the Desmaninae, a consideration not very surprising since the Desmaninae were previously thought to exist in North America (Shotwell, 1956). However, Hutchison (1968) and Wilson (1960) have proved that the Uropsilinae do occur in North America, so assignment to this subfamily seems more practical at this stage. Known uropsiline molars of *Mystipterus* are smaller, and it appears, more brachydont than this highly sectorial tooth. This probably reflects a divergent uropsiline line attaining extreme hypsodonty in the Miocene.

Order Rodentia Bowdich, 1821
Family Sciuridae Gray, 1821
Tamias? species

Material.—SDSM 8699, P^4; SDSM 8697, two P_4; SDSM 8698, one lower molar.

Description.—These teeth are worn. They are placed here primarily because of their small size. The upper premolar, although worn, shows some hint of a metaconule as in the *Tamias* from the Sharps Formation (Black, 1963). One P_4 is moderately worn so the trigonid can be observed. The metaconid and protoconid are closely appressed and, in conjunction with a very small anteroconid, they form a trigonid basin. No mesoconid or mesostylid exists. The lower molar has a well developed trigonid basin and no mesoconid.

The small anteroconid and trigonid basin development are unlike any other described specimens of *Tamias* P_4. This makes reference hypothetical.

Perhaps these teeth represent another form, but better material is needed for substantiation. Measurements, SDSM 8699, P^4, AP = 1.10; Tr = 1.20. SDSM 8697, AP; N = 2, observed range = 1.20, $\bar{X}$ = 1.20; Tr: observed range = 1.02–1.09, $\bar{X}$ = 1.06. SDSM 8698, M_1 or M_2, AP = 1.29; Tr = 1.00.

cf. *Miospermophilus* species Black, 1963

Material.—SDSM 8694, five P^4; SDSM 8695, four M^1 or M^2; SDSM 8710, left M^1 or M^2; SDSM 8696, two M^3; SDSM 8691, four P_4; SDSM 8692, six M_1 or M_2; SDSM 8711, right M_1 or M_2; SDSM 8693, four M_3.

Description.—The lower premolar is similar to that of *Miospermophilus* in its small size (Table 7), poorly developed entoconid, and lack of mesoconid and mesostylid. The anterior portion does show some difference. In two specimens, no anteroconid is present. It appears in another, which may be deciduous, and the fourth is broken. A distinct metalophid is not developed.

Lower M_1 or M_2 has a small trigonid, normally with an enclosed basin. There is some variation in the completeness of the metalophid. Variation also appears in the presence of a mesoconid and metastylid. The entoconid is usually well formed.

M_3 does not have a trigonid basin and the entoconid is incorporated into the posterolophid. No mesoconid or mesostylid is present.

The upper premolar and M^1 or M^2 are small and delicate. The protoloph and metaloph are subparallel joining a transversely expanded protocone. Anterior and posterior cingula are well developed with the anterior being the more prominent. They make an abrupt change of direction before joining the protocone. This results in a more quadrate shaped tooth outline. Mesostyles may be present, but are usually small. There are no protoconules or metaconules. The anterior cingulum of M^3 is weakly developed, the metaloph is complete, and a mesostyle appears on the unworn specimen.

Discussion.—These teeth are smaller and more delicate than those of *M. bryanti* (Wilson) from Quarry A or of *M. wyomingensis* Black from Split Rock. They are closer in size to "cf. *Miospermophilus* sp." from the Batesland Formation (Martin, 1976). They differ from *M. bryanti* in having a better developed entoconid and the presence of mesoconids on the lower molars, and the lack of metaconules on the upper molars. They differ from *M. wyomingensis* in having a better developed entoconid, a curved anterior cingulum on the trigonid, usually a complete metalophid, subparallel lophs, lack of a metaconule, and a mesostyle in M^3. The teeth are more like those from the Batesland Formation, but differ in that the upper premolar does not possess a metaconule and the lophs are not V-shaped. They differ from *Miospermophilus* species of the Vedder locality, Hemingfordian, Santa Barbara County, California (Hutchison and Lindsay, 1974) in subparallel lophs in the upper molars and poorly developed entoconid on P_4.

Table 7.—*cf.* Miospermophilus.

Museum no., tooth	Measurement	N	Observed range	Mean	SD	C.V.
SDSM 8691, P_4	AP	4	1.32–1.45	1.39	±0.05	3.60
	Tr	4	1.01–1.30	1.21	±0.13	10.74
SDSM 8692, M_1 or M_2	AP	6	1.38–1.52	1.47	±0.06	4.08
	Tr	7	1.30–1.69	1.54	±0.14	6.49
SDSM 8693, M_3	AP	5	1.50–1.80	1.61	±0.12	7.45
	Tr	5	1.58–1.79	1.65	±0.08	4.85
SDSM 8694, P^4	AP	5	1.25–1.42	1.35	±0.07	5.19
	Tr	5	1.40–1.60	1.47	±0.08	5.44
SDSM 8695, M^1 or M^2	AP	5	1.51–1.60	1.56	±0.05	3.21
	Tr	5	1.79–1.91	1.86	±0.04	2.15
SDSM 8696, M^3	AP	1		1.61		
	Tr	1		1.70		

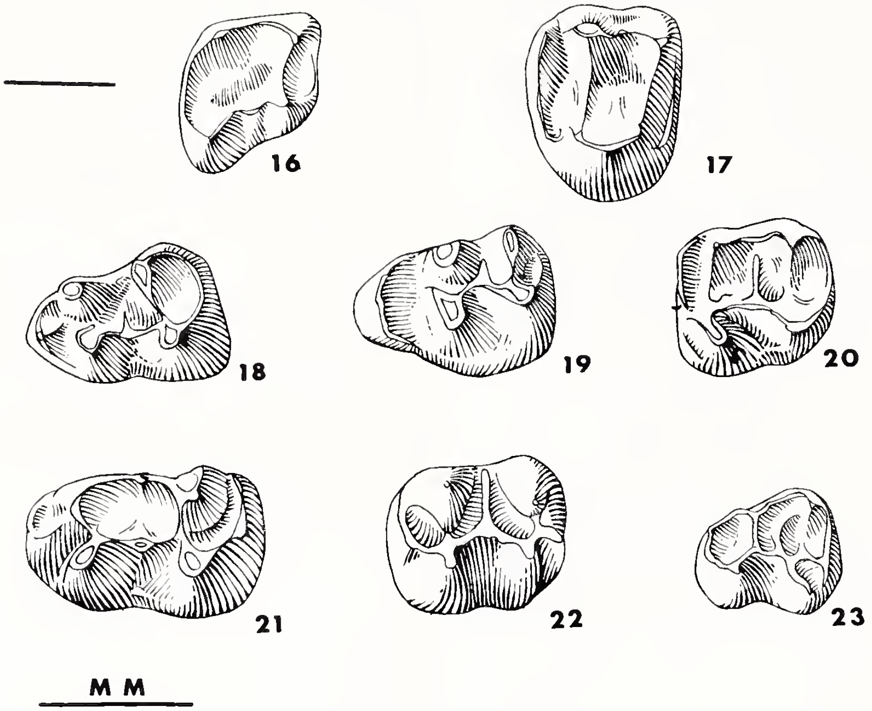
This form might represent a new genus related to *Miospermophilus* based on the subparallel lophs, cingular structure, and lack of metaconules on the upper dentition. More and better material is needed to justify this contention. At any rate, it is a form related to *Miospermophilus* and may represent a more upland adaptation. Of particular significance in this regard is that *Protospermophilus* is absent in BBQ II. This genus has been found in and may be restricted to a riparian environment such as that demonstrated by Quarry A and Flint Hill North.

Family Cricetidae Rochebrune, 1883

Leidymys species
Figs. 18–20

Material.—SDSM 67142, left M_1, broken left M_1; SDSM 67143, four left M_2, two right M_2; SDSM 8684, three M_3; SDSM 8705, left M^1; SDSM 8685, left M^1; SDSM 8686, two right M^2; SDSM 8706; left M^2.

Description.—The M_1 are brachydont teeth of about the same size as *Leidymys* species from the Batesland Formation (Martin, 1976). A single anteroconid is connected directly to the protoconid by a faint crest on one M_1, whereas a crest from the metaconid and one from the protoconid join to form a single crest, which intersects the anteroconid me-



Figs. 16–23.—16) cf. *Miospermophilus* species, SDSM 8711, right M_1 or M_2. 17) cf. *Miospermophilus* species, SDSM 8710, left M^1 or M^2. 18) *Leidymys* species, SDSM 67142, left M_1. 19) *Leidymys* species, SDSM 8705, left M^1. 20) *Leidymys* species, SDSM 8706, left M^2. 21) Cricetidae, small species, SDSM 8707, left M_1. 22) Cricetidae, small species, SDSM 8688, right M_2. 23) Cricetidae, small species, SDSM 8708, right M_3. The short scale refers to Figs. 16–20. Scales = 1 mm.

dially on the other specimen. The ectolophid extends from the protoconid to the midpoint of the hypolophid. A small mesoconid exists on the ectolophid and sends a short spur lingually, which is not a complete mesolophid. The metaconid and protoconid are opposite one another, as are the entoconid and hypoconid. A posterior cingulum is present.

Second lower molars are similar to *Leidymys alicae* (Black) from the Flint Creek local fauna in Montana (Black, 1961), and to *Leidymys* species from the Batesland Formation (Martin, 1976), but show some variations of the anterior cingulum. It is connected to the metaconid and protoconid by individual crests. A medial connection from the metaconid to the cingulum is present. The posterior arm of the protoconid is usually larger than the mesolophid and extends almost to the lingual border of the tooth. However, the converse is true in one specimen.

Table 8.—Leidymys *species.*

Museum no, tooth	Measurement	N	Observed range	Mean	SD	C.V.
SDSM 67142, M_1	AP	1		2.01		
	Tr	1		1.40		
SDSM 67143, M_2	AP	5	1.72–1.85	1.77	±0.06	3.39
	Tr	6	1.40–1.51	1.43	±0.05	3.50
SDSM 8684, M_3	AP	3	1.52–1.79	1.68	±0.14	8.33
	Tr	3	1.30–1.35	1.33	±0.03	2.26
SDSM 8685, M^1	AP	2	2.10–2.18	2.14	±0.06	2.80
	Tr	2	1.45–1.48	1.47	±0.02	1.36
SDSM 8686, M^2	AP	3	1.72–1.89	1.80	±0.09	5.00
	Tr	3	1.50–1.61	1.55	±0.06	3.87

The M_3's are almost identical to those of *Leidymys alicae,* but the mesoconid is more pronounced on the Rosebud specimens.

On M^1 a large, isolated anterocone is present. The paracone and protocone are directly opposite, as are the metacone and hypocone. On one specimen protolophule I is incomplete, while on the other protolophule II is incomplete. The mesoloph almost reaches the buccal border of the tooth.

The M^2's are identical to those from the Batesland Formation. Among the BBQ II specimens variations are also seen in the length of the mesoloph. This character seems especially variable among these cricetid species.

Table 9.—*Cricetidae, small species.*

Museum no., tooth	Measurement	N	Observed range	Mean	SD	C.V.
SDSM 8687, M_1	AP	2	1.71–1.75	1.73	±0.03	1.73
	Tr	2	1.10–1.12	1.11	±0.01	0.90
SDSM 8668, M_2	AP	1		1.35		
	Tr	1		1.10		
SDSM 8669, M_3	AP	2	1.05–1.11	1.08	±0.04	3.74
	Tr	2	0.95–1.01	0.98	±0.04	4.08
SDSM 8690, M^2	AP	4	1.08–1.35	1.24	±0.12	9.68
	Tr	4	1.08–1.30	1.17	±0.10	8.55

Discussion.—These molars represent another occurrence of Hemingfordian cricetids and are part of an evolutionary line surviving from the Oligocene into the early Miocene. In South Dakota, the genus is known from the Sharps Formation by *Leidymys blacki* (Macdonald) (J. R. Macdonald, 1963); from the Monroe Creek Formation by SDSM 64159-1, an M^1 described by L. J. Macdonald (1972) as "Cricetid, genus undetermined"; from the Rosebud Formation, by these specimens; and from the overlying Batesland Formation (Martin, 1976). This line might eventually be traced into *Copemys* Wood, but our present knowledge is not conclusive. The Hemingfordian *Leidymys* does not exhibit the staggered cusps characteristic of Barstovian *Copemys.*

The BBQ II species is almost identical with that described from the Batesland Formation and is close to the Monroe Creek specimen. More complete dentitions are required before specific distinctions can be made. The Rosebud teeth differ from *Leidymys alicae* in their smaller size, anteroconid structure of M_1, and the absence of a mesolophid on M_1.

Cricetidae, small species

Figs. 21–23

Material.—SDSM 8690, left M^2; SDSM 8687, two M_1; SDSM 8707, left M_1; SDSM 8688, right M_2; SDSM 8708, right M_3; SDSM 8689, left M_3.

Description.—This is another cricetid with a brachydont dentition. As measurements indicate (Tables 8–9), it is much smaller than the BBQ II *Leidymys* species. Size, coupled with unique morphology, indicates a new form, but we have insufficient material to name the cricetid.

The anteroconid structure of M_1 is similar to that described for *Leidymys.* There are two crests originating from the metaconid and protoconid directed anteriorly. They may either join together before intersecting the anteroconid, or each will intersect it individually. In both cases, the intersection is anteromedial. A slight mesoconid is present, but does not display the internal spur as does *Leidymys.* There is a small bulge in the enamel at the base of the metaconid, which is suggested on the heavily worn specimen.

The M_2 is unworn and appears unusual for this normally conservative tooth. Perhaps it does not belong to this species, but it does fit the size range. It does not possess roots and might not be a fully formed tooth. The anterior crests (metalophulid I) join anteromedially in a small anteroconid. No anterior cingulum is present as in most other cricetids. The posterior arm of the protoconid reaches the lingual edge of the tooth, and no mesoconid is present. A small hypoconulid is present on the broken M_2 in a dentary fragment containing an M_3.

The M_3's are similar to those of *Leidymys,* except that the posterior arm of the protoconid (metalophulid II) varies. It is directed anterad toward the metaconid and actually joins it in one case. This results in a fossettid upon wear. A slight bulge exists on the ectolophid, but is not a true mesoconid.

Unfortunately, no M^1 specimens are in the collection, but M^2 shows peculiarities. It has both a lingual and labial projection of the anterior cingulum but the labial spur is connected to the paracone and the lingual spur to the protocone. Only a mesocone and metastyle are present instead of a mesoloph, and a prominent posterior cingulum exists.

Discussion.—The small size and peculiar structure of the mesocone on M^2, the anterior cingulum of the M^2, and the metalophulid II of M_3, probably indicate a new taxon. Additional specimens, especially of M^1 are needed before a new name can be assigned. It appears to have arisen from the brachydont *Leidymys* stock but exhibits dental adaptations parallel to some zapodids.

SUMMARY

The BBQ II fauna is of early Hemingfordian age and is most similar to the Marsland and Quarry A faunas.

The environment of deposition of the quarry is non-riparian as indicated by the lack of stream border forms such as *Plesiosorex,* castorids, aplodontids, mylagaulids, and *Protospermophilus.*

Among the Insectivora, the range of the Geolabididae is extended into the Hemingfordian. A new hedgehog, *Hibbarderix,* is found in South Dakota and adds to the diversity of the Miocene erinaceids. *Parvericius* is suspected from the locality. Shrews are represented by *Wilsonosorex* and *Antesorex.* One upper molar might represent a desmanine or uropsiline talpid.

Cricetids are not absent in the Hemingfordian, but appear continuously from the Oligocene to the Middle Hemingfordian. *Leidymys* and an unnamed new genus are present at BBQ II. The Sciuridae are represented by *Tamias* and cf. *Miospermophilus.*

LITERATURE CITED

Black, C. C. 1961. Fossil mammals from Montana. Pt. 1. Additions to Late Miocene Flint Creek local fauna. Ann. Carnegie Mus., 36:69–76.

———. 1963. A review of the North American Tertiary Sciuridae. Bull. Mus. Comp. Zool., Harvard Univ., 130:109–248.

Cook, H. J. 1965. Runningwater Formation, Middle Miocene of Nebraska. Amer. Mus. Novit., 2227:1–7.

Engesser, B. 1972. Die obermiozäne Säugetierfauna von Anwil (Baselland). Naturforsch. Ges. Baselland, Tätigkeitsber., 28: 37–363.

———. 1975. Revision der Europäischen Heterosoricinae (Insectivora, Mammalia). Eclogae Geol. Helv., 68:649–671.

Green, M. 1972. Lagomorpha from the Rosebud Formation, South Dakota. J. Paleont., 46:377–385.

———. 1977*a*. Neogene Zapodidae (Mammalia: Rodentia) from South Dakota. J. Paleont., 51:996–1015.

———. 1977*b*. A new species of *Plesiosorex* (Mammalia, Insectivora) from the Miocene of South Dakota. N. Jb. Geol. Palaont. Mh., 4:189–198.

Green, M., and J. E. Martin. 1976. *Peratherium* (Marsupialia: Didelphidae) from the Oligocene and Miocene of South Dakota. Athlon: Essays in Palaeontology in Honour of Loris Shano Russell. Roy. Ontario Mus. Life Sci., Misc. Publ., 155–168.

Harksen, J. C., and J. R. Macdonald. 1969. Guidebook to the major Cenozoic deposits of southwestern South Dakota. South Dakota Geol. Surv., Guidebook 2:ix + 1–103.

Hutchison, J. H. 1968. Fossil Talpidae (Insectivora, Mammalia) from the later Tertiary of Oregon. Bull. Mus. Nat. Hist., Univ. Oregon, 11:1–67.

———. 1972. Review of the Insectivora from the early Miocene Sharps Formation of South Dakota. Contr. Sci., Los Angeles County Mus., 235:1–16.

———. 1974. Notes on type specimens of European Miocene Talpidae and a tentative classification of Old World Tertiary Talpidae (Insectivora: Mammalia). Geobios, 7:211–256.

Hutchison, J. H., and E. H. Lindsay. 1974. The Hemingfordian mammal fauna of the Vedder Locality, Branch Canyon Formation; Santa Barbara County, California. Part 1: Insectivora, Chiroptera, Lagomorpha, and Rodentia (Sciuridae). PaleoBios, 15:1–19.

Koerner, H. E. 1940. The geology and vertebrate paleontology of the Fort Logan and Deep River Formations of Montana. Amer. J. Sci., 238:837–862.

Lillegraven, J. A., McKenna, M. C., and L. Kristalka. 1981. Evolutionary relationships of middle Eocene and younger species of *Centetodon* (Mammalia, Insectivora, Geolabididae) with a description of the dentition of *Ankylodon* (Adapisoricidae). Univ. Wyoming Publ., 45:1–115.

Macdonald, J. R. 1963. The Miocene faunas from the Wounded Knee area of western South Dakota. Bull. Amer. Mus. Nat. Hist., 125:139–238.

———. 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Bull. Los Angeles County Mus., Sci., 8:1–82.

Macdonald, L. J. 1972. Monroe Creek (early Miocene) microfossils from the Wounded Knee area, South Dakota. South Dakota Geol. Survey Rept. Invest., 105:iii + 1–43.

McKenna, M. C. 1960. The Geolabidinae. A new subfamily of early Cenozoic erinaceoid insectivores. Univ. California Publ., Geol. Sci., 37:131–164.

Martin, J. E. 1976. Small mammals from the Miocene Batesland Formation of South Dakota. Contr. Geol., Univ. Wyoming, 14:2:69–98.

———. 1978. A new and unusual shrew (Soricidae) from the Miocene of Colorado and South Dakota. J. Paleont., 52:636–641.

Rich, T. H. V., and D. L. Rasmussen. 1973. New North American hedgehogs (Mammalia: Insectivora). Occ. Papers Mus. Nat. Hist., Univ. Kansas, 21:1–54.

Rich, T. H. V., and P. V. Rich. 1971. *Brachyerix,* a Miocene hedgehog from western North America, with a description of the tympanic regions of *Paraechinus* and *Podogymnura.* Amer. Mus. Novit., 2477:1–58.

Shotwell, J. A. 1956. Hemphillian mammalian assemblage from northeastern Oregon. Bull. Geol. Soc. Amer., 67:717–738.

Storer, J. E. 1975. Tertiary mammals of Saskatchewan. Part III: The Miocene fauna. Life Sci. Contr. Roy. Ontario Mus., 103:1–134.

Voorhies, M. R. 1973. Early Miocene mammals from northeastern Nebraska. Contrib. Geol., Univ. Wyoming, 12:1–10.

Wilson, R. W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. Univ. Kansas Paleont. Contr. Vertebrata, 7:1–92.

Note Added in Proof

This contribution was originally submitted in the Spring of 1979. Many taxonomic, range, and interpretative revisions such as those of Engesser (1979), Rensberger (1980), and Rich (1980) are not included. As many revisions as practical were made in the proofs, but many views represent those formulated with the state of knowledge at the time of submittal.

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LATE CENOZOIC LEPORIDAE (MAMMALIA, LAGOMORPHA) FROM THE ANZA-BORREGO DESERT, SOUTHERN CALIFORNIA

John A. White

ABSTRACT

The leporids from the Palm Spring Formation in the Anza-Borrego Desert of Southern California are represented by two archaeolagines, *Hypolagus vetus* and *Pewelagus dawsonae* new genus and species, and three leporines, *Nekrolagus* species, *Sylvilagus hibbardi* new species, and specimens of a large, advanced leporid. In this stratigraphic section, the archaeolagines and *Nekrolagus* species occur in the Late Blancan and Irvingtonian, and the large, advanced leporid in the Irvingtonian.

H. vetus is ecologically replaced in the section by *S. hibbardi*, and the two species are referred to the cottontail ecomorph. *Palaeolagus hypsodus* is referred to the rock rabbit ecomorph, and *Prolagus sardus* and *Kenyalagomys* are referred to the cottontail ecomorph.

It was impossible to refer the large, advanced leporid to either *Sylvilagus* or *Lepus*, as size and enamel patterns on P_3 cannot be used as criteria for this purpose.

INTRODUCTION

The fossil vertebrates dealt with in this paper were obtained in the Anza-Borrego Desert from sites occurring in more than 2,325 m (7,622 feet) of that part of the Palm Spring Formation (Woodring, 1931; Dibblee, 1954; Woodard, 1963) exposed in the Vallecito Creek and Fish Creek Wash areas in the Anza-Borrego Desert State Park in eastern San Diego County, California. Specimens of leporids have been recovered from 82 stratigraphic levels in that part of the section, which is in continuous sequence, is referred to by Downs and White (1968) as the "type section," and extends in time from early Blancan Pliocene to late Irvingtonian early Pleistocene (Berggren and Van Couvering, 1974; Opdyke et al., 1977; and Marshall et al., 1979).

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MATERIALS AND METHODS

Most of the specimens used in this study are in the collections of the Natural History Museum of Los Angeles County, Department of Vertebrate Paleontology (LACM). Others are housed at the San Diego Museum of Natural History (SDMNH), Imperial Valley College Museum (IVCM), Department of Zoology, University of Arizona (UADZ), and Idaho Museum of Natural History (IMNH).

All measurements were made with dial calipers calibrated to 0.1 mm. Anatomical terminology is that of Craigie (1948).

The specimens of leporids discussed herein are more complete than usual, and the descriptions of these specimens are relatively brief. This briefness of description reflects the discovery that lagomorphs are referable to ecomorphs (White and Keller, 1983). These authors define an ecomorph to include groups of organisms whose morphological similarities imply ecological preference irrespective of systematic relationships.

Specimens of the post-cranial skeleton are, for the most part, not analyzed in this paper, pending completion of analysis of variation in post-cranial elements in living forms.

SYSTEMATIC ACCOUNTS

Order Lagomorpha Brandt 1855
Family Leporidae Gray 1821
Subfamily Archaeolaginae Dice 1929

Genus ***Hypolagus*** Dice 1917
Hypolagus vetus (Kellogg)
(Figs. 1–3)

Lepus vetus Kellogg, Univ. California Pub. Bull. Dept. Geol. 5(29):436, 13 July 1910.

Hypolagus vetus, Dice, Univ. California Pub. Bull. Dept. Geol. 10(12):181, 23 March 1917.

Referred specimens.—Unless otherwise specified, locality and specimen numbers listed below are in the collections of the Natural History Museum of Los Angeles County. Localities are listed in numerical order, italicized, and followed by specimen numbers.

Locality *1920:* 7434 fragmentary skull with complete upper and lower dentitions, with distal ⅓ humerus and proximal end of tibia; *1923:* 24965 left mandibular fragment with P_3–P_4; *3238:* 40139 right mandibular fragment with P_3–M_3; *4267:* 115101 left mandibular fragment, immature specimen; *6524:* 24670 femoral and tibial fragments; *6529:* 13742 P_3; *6546:* 23417 astragalus and calcaneum; *6552:* 16859 left mandibular fragment with P_3–P_4; *6553:* 24754 cranial fragments; *6557:* 23431 cranial fragments, four metatarsals, and other fragments, 24973 fragmentary skeletal parts; *6564:* 13729 cranium with zygomatic arches and P^2s missing, humerus and ulnar fragments; *65115:* 24972 right mandibular fragment with P_3–M_3; *65116:* 39459 fragment of distal femur; *65117:* 24665 pelvis and skeletal fragments; *65171:* 24969 cranial fragment with complete dentition; *65177:* 23444 cranium with basicranium missing; *6604:* 23422 distal humeral fragment, 23447 cranium with right zygomatic arch missing, atlas in articulation, 24957 articulated pes and other fragments; *66163:* 17687 P^2; *66165:* 24966 rostrum with incisors and P^3–P^4, 24967 palate with complete dentition, 24968 mandibular fragment with left P_3, 23425 astragalus, calcaneum, proximal ends of femora, humerus, scapula, distal ends of femora with articulating tibiae; *6715:* 17648 skull with left zygomatic arch missing, 17668 cranial fragments, 39461 distal end of pes with metatarsals; *6719:* 17667 left mandibular fragment with P_3–P_4; *6724:* 24750 right mandibular fragment with P_3; *6748:* 24719 three articulated pedes with metatarsals, tarsus, and other fragments; *6814:* 20923 skull with zygomatic arches missing and fragmentary mandible, complete dentitions, 24578 skeletal fragments, 24579 mandible with I, P_3–M_2, posterior end missing, 24580 skeletal fragments, 24581 cranial fragments, 24585 cranial fragments; *6821:* 39462 distal

Table 1.—*Statistical data relating to* Hypolagus vetus *from the Anza-Borrego Desert section.*

Measurement	M	N	SD	SE	OR
Anterior surface I^1* to inyon	70.65	2	—	—	62.9–78.4
Anterior surface I^1 to foramen magnum	67.3	1	—	—	—
Anterior surface I^1 to bony palate	23.2	2	—	—	19.4–27.0
L palatine foramen	19.17	2	—	—	18.3–19.8
W palatine foramen	6.88	5	.68	.30	6.3–8.0
Least APL bony palate	5.33	8	.82	.27	4.6–6.8
Bony palate to basisphenoid	22.95	2	—	—	22.7–23.2
W choana posterior to bony palate	6.32	5	.99	.44	5.1–7.6
L basioccipital	10.33	3	—	—	9.3–12.0
APL tympanic bulla	12.20	6	1.09	.41	10.7–13.2
W tympanic bulla	8.84	5	1.42	.58	7.6–10.7
W between bullae	6.83	3	—	—	6.1–7.5
Inyon to foramen magnum	7.30	3	—	—	6.4–8.5
W across occipital condyles	12.10	4	—	—	10.7–13.0
Least postorbital constriction	12.10	1	—	—	—
W across supraorbital ridges	20.00	1	—	—	—
Depth anterior end zygomatic arch	4.93	6	.69	.26	4.1–5.7
W skull anterior end zygomatic arches	30.90	5	2.47	1.10	26.9–33.2
Diastema I^2–P^2	18.77	3	—	—	15.7–22.7
L row upper cheek teeth at wear surface	11.71	8	.39	.13	11.0–12.2
L row upper cheek teeth at alveoli	14.00	11	.79	.23	13.0–15.5
APL I^1	1.78	5	.16	.07	1.5–1.9
W I^1	2.59	7	.32	.11	2.1–3.0
W I^2	1.36	4	—	—	1.0–1.6
APL P_3	2.92	13	.22	.06	2.6–3.3
W P_3	2.69	16	.17	.04	2.5–3.1
Diastema I_1–P_3	15.80	5	1.29	.53	13.9–17.0
L row lower cheek teeth at wear surface	11.98	4	—	—	11.0–12.5
L row lower cheek teeth at alveoli	14.45	6	1.15	.44	13.0–16.1

* APL = anteroposterior length, L = length, W = width, subscripts refer to lower dentition, superscripts refer to upper dentition, numbers refer to individual teeth in a series, I = incisor, and P = premolar.

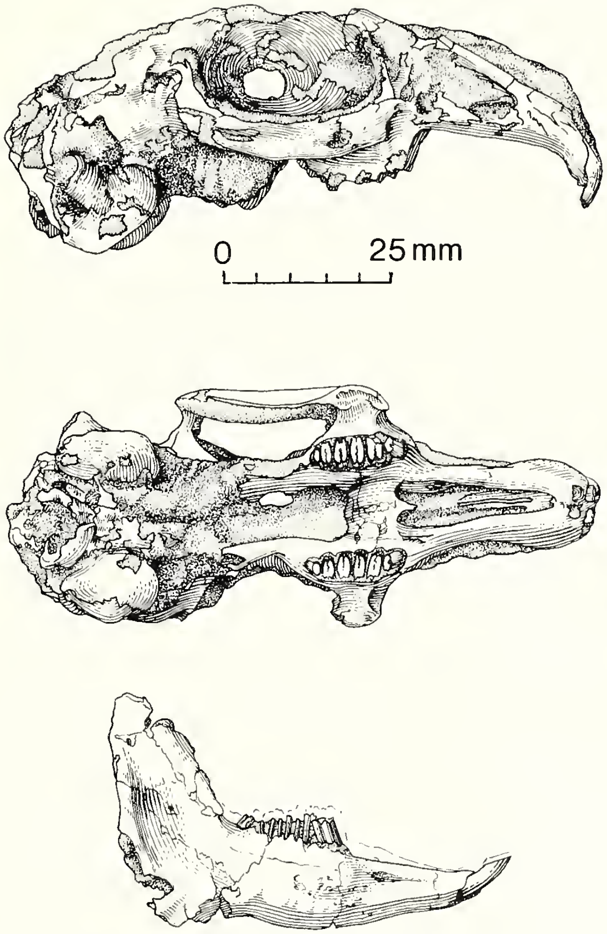

Fig. 1.—Right-lateral and ventral views of cranium and right-lateral view of mandible of *Hypolagus vetus,* specimen number 24974 from LACM locality 6822. Drawn by Erica H. Craig.

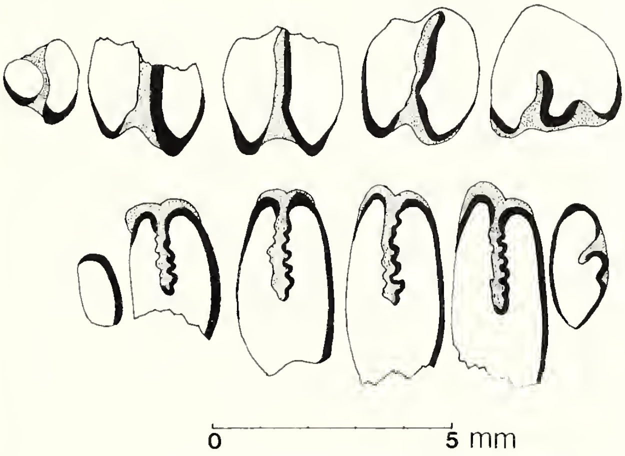

Fig. 2.—Upper and lower occlusal enamel patterns of cheek teeth of *Hypolagus vetus,* specimen 24974 from LACM locality 6822.

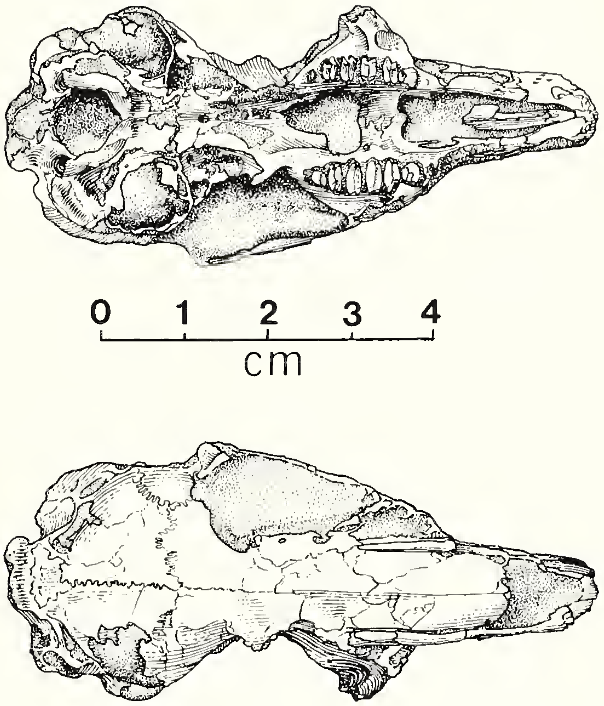

Fig. 3.—Dorsal and ventral views of the cranium of *Hypolagus vetus,* specimen 20445 from SDMNH locality L1959. Drawn by Erica H. Craig.

tibia; *6822:* 24974 skull with left zygomatic arch missing, posterior end of mandibles missing, complete dentitions, and fragmentary skeletal parts; *6864:* 24971 mandibular fragment with P_3–M_1, 20928 maxillary fragment with P^2, P^3 missing; *7068:* 24669 skull with zygomatic arches and right basicranium and right mandibular ramus missing, fragments of scapula, right and left proximal radius and ulna articulated with distal right and left humeri.

IVCM: *GJM 1204:* 1274 mandibular fragment with P_3; *341:* 1276 left mandibular fragment with P_3–M_2.

SDMNH: *L1959:* 20445 cranium with right zygomatic arch missing.

Specific characters.—Size medium (Table 1), near *Sylvilagus floridanus* and *Lepus americanus.* P_3 with thick enamel on anterior edge of postero-external reentrant which is directed posteriad (Hibbard, 1969). P^2 ovoid in cross section with a deep anterior reentrant on lingual one-third, and a shallow one on labial one-third of tooth, both of which extend to base of crown. Skull proportions essentially as in *S. floridanus* and *L. americanus,* making this species referrable to the cottontail ecomorph (White and Keller, 1983).

Geologic age and distribution.—The occurrence of *H. vetus* from the Late Hemphillian of Thousand Creek, Nevada, to the Blancan of the Palm Spring

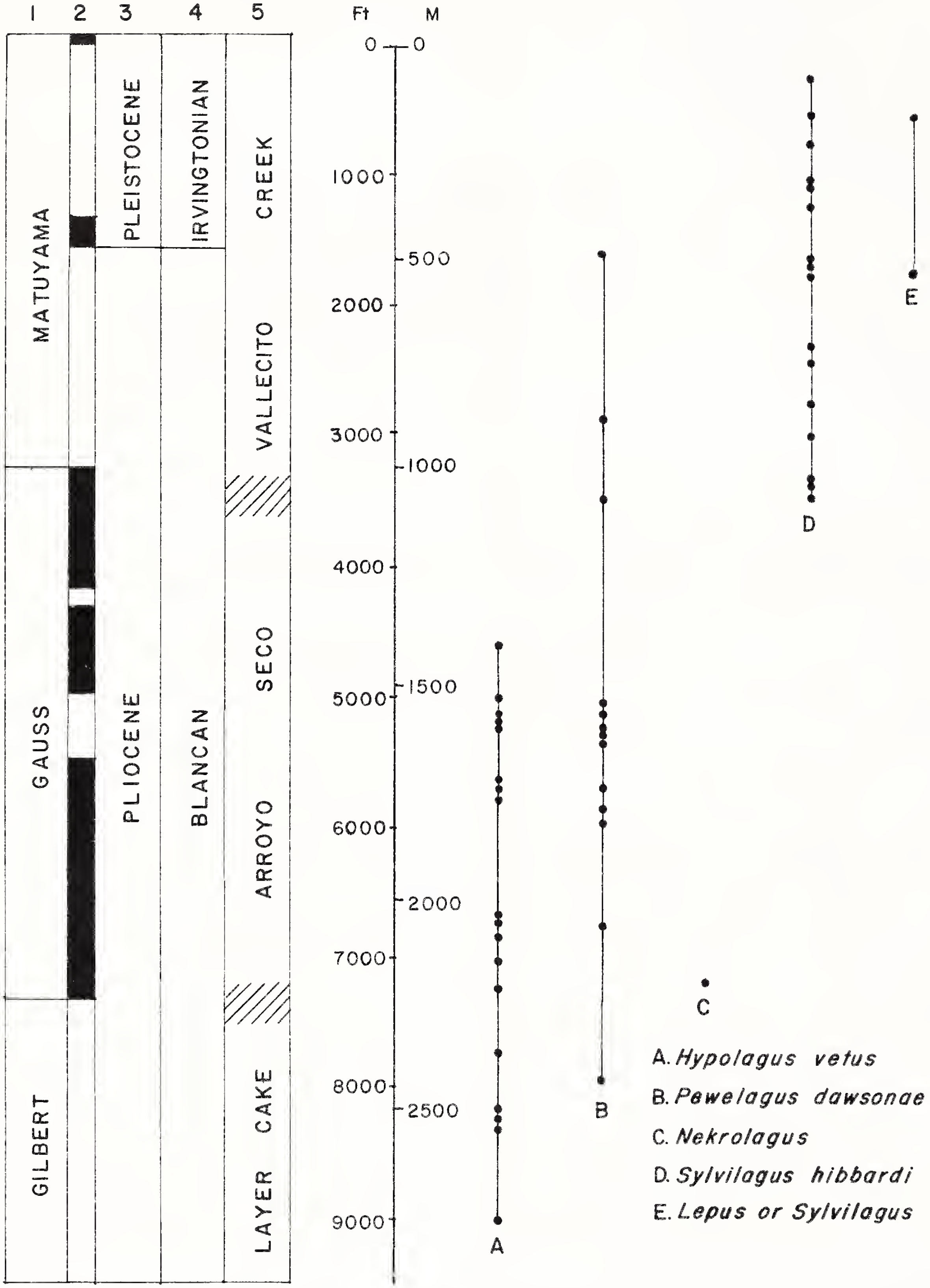

Fig. 4.—Stratigraphic ranges of leporids from the Anza-Borrego Desert section. (1) and (2) paleomagnetic scale; (3) epochs; (4) mammalian provincial ages; and (5) local faunas.

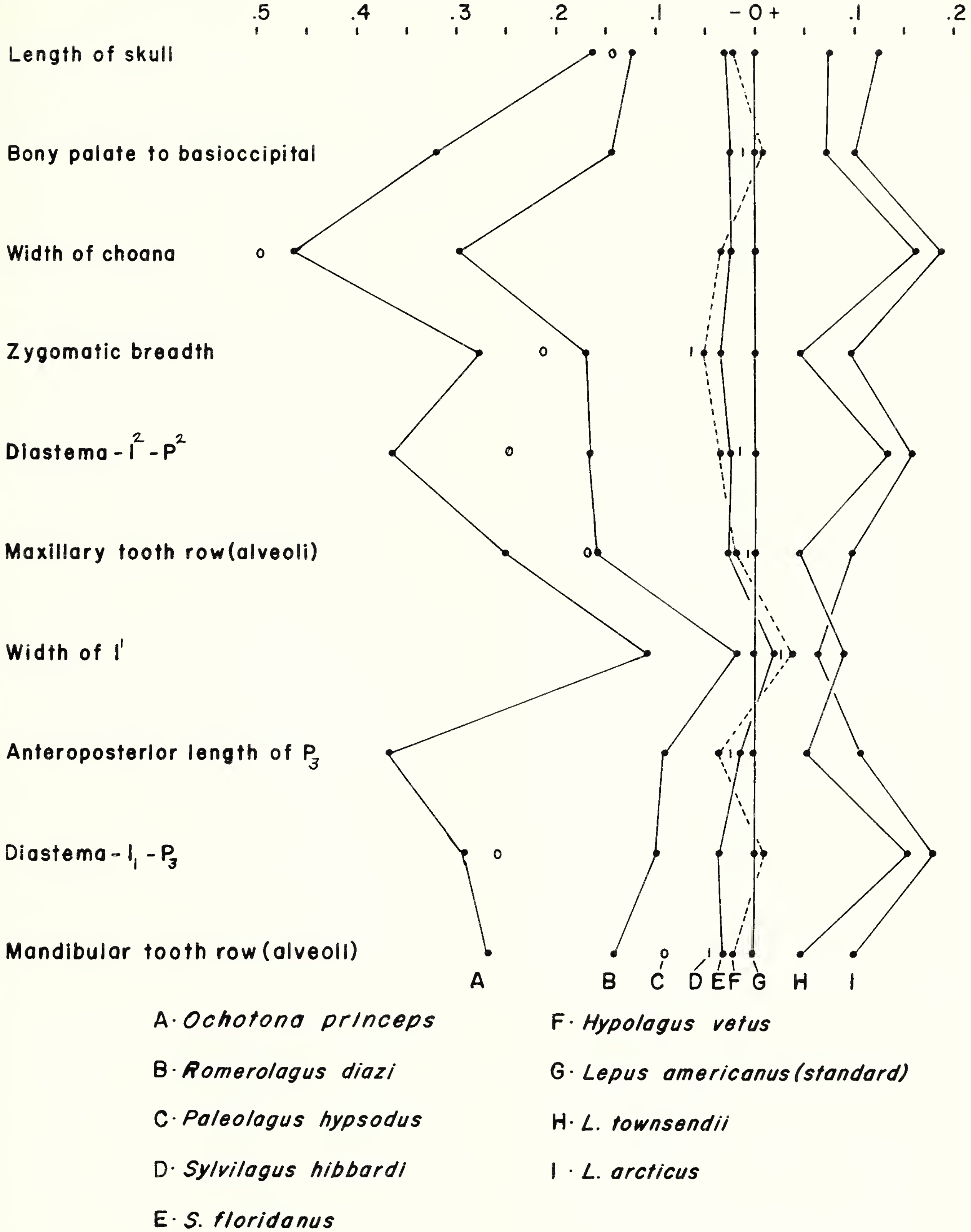

Fig. 5.—Ratio diagram (Simpson et al., 1960) of nine species of lagomorphs, comparing skull proportions.

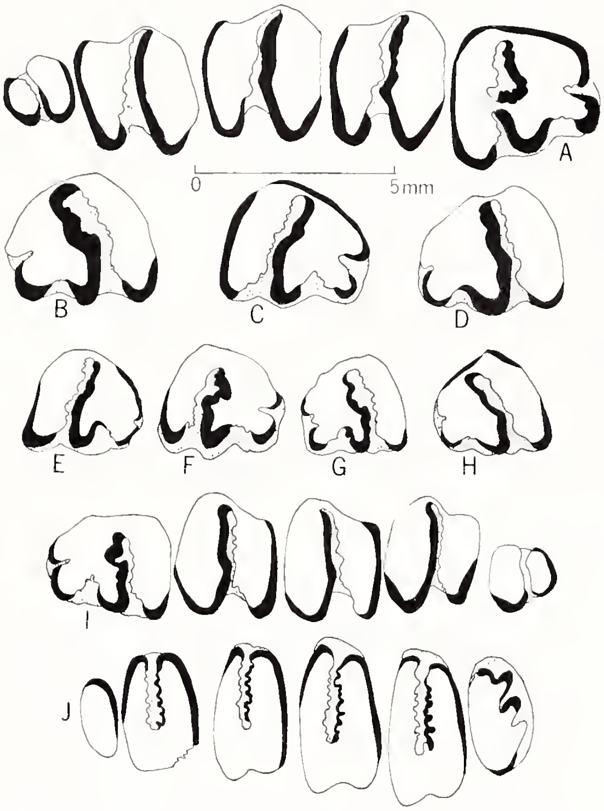

Fig. 6.—Occlusal enamel patterns of leporine cheek teeth. A and C, leporine, genus and species indeterminate: A, specimen 1275 from IVCM locality 113; C, specimen 24839 from LACM locality 1906; B, *Sylvilagus cunicularius*, Recent (UADZ 5133); D, *Lepus townsendii*, Recent (IMNH R326); E, *S. floridanus*, Recent (IMNH R582); H, *L. americanus*, Recent (IMNH 7011); F, *S. hibbardi* new species specimen 24985 from LACM locality 1114; G, specimen 6760 from LACM locality 1469; J, specimen 4429 from LACM locality 1588; and I, specimen 4394 (holotype) from LACM locality 1615.

Formation in the Anza-Borrego Desert section provides the only reasonably certain stratigraphic range for this species. All other specimens from other localities, which range in time from Barstovian to the Blancan, have been tentatively referred to this species, and are in need of reexamination.

Table 2.—*The numbers of plications in the enamel of hypostriae in upper cheek teeth of* Hypolagus vetus.

Tooth and numbers of specimens (N)	Observed ranges	
	Anterior enamel	Posterior enamel
P^3 (9)*	7–9	0–4
P^4 (9)	8–10	0–5
M^1 (8)	7–11	0–3
M^2 (8)	6–10	0–5

* Abbreviations as explained in Table 1.

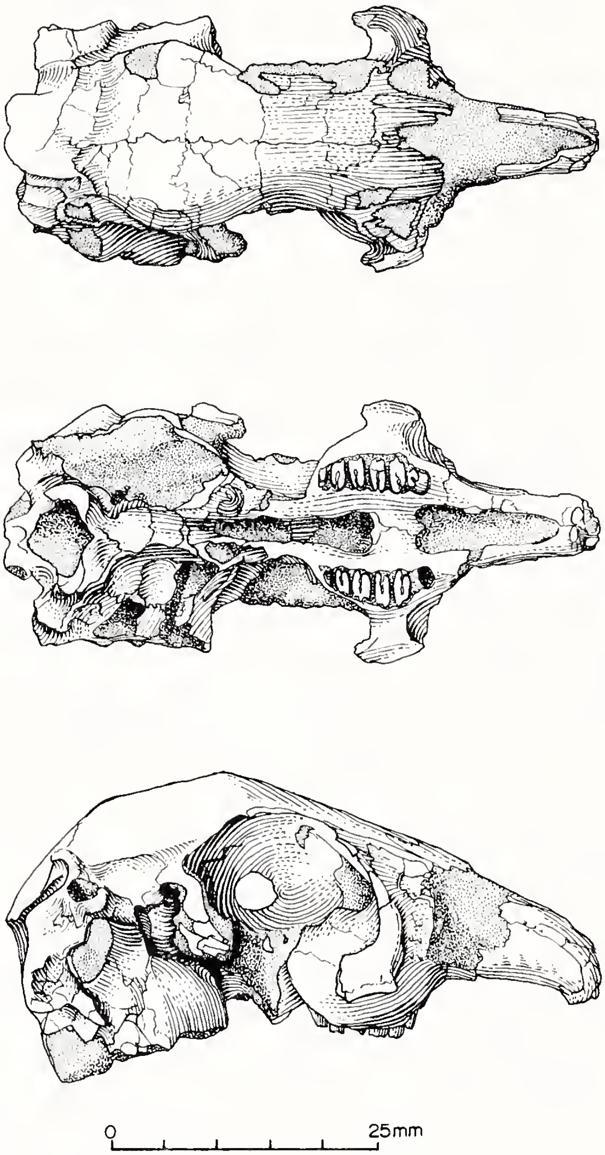

Fig. 7.—Dorsal, ventral, and right-lateral views of the cranium of *Pewelagus dawsonae* new species, specimen 24664 (holotype) from LACM locality 6583. Drawn by Erica H. Craig.

In the Anza-Borrego Desert section this species occurs from 1,430 m (3,420 feet) to 2,964 m (9,720 feet) below top of section, and entirely in the Blancan (Fig. 4).

DESCRIPTION

Skull.—The skull in *H. vetus* is remarkably similar to the skulls of *S. floridanus* and *L. americanus* (Fig. 5). The interparietal bone is visible.

Dentition.—P^2 with deep reentrant at lingual one-third of tooth and extends posterolabiad; a shallow reentrant inflected at labial one-third of tooth. I^1 essentially as in *S. floridanus*, but I^2 rounded in cross section and slightly compressed anteroposteriorly. P^3–M^2 with thin enamel on hypostriae, which are variably crenulated (Table 2). M^3 with thick enamel only on its anterior and labial sides.

Labial side of P_3 faces laterad and slightly anteriad. Anteroexternal reentrant shallow. Posteroexternal reentrant extends linguad and slightly more than half way across occlusal surface; thick enamel on anterior margin usually strongly sigmoid, thickness in lingual portion about the same as on labial portion, or may be thinned out lingually.

Appendicular skeleton.—Other species of leporids occur with *H. vetus* in the Anza-Borrego Desert section. Therefore, any post-cranial material, unless associated with cranial materials, can only be assigned doubtfully to this species. Scapular fragments seem to be about the size of the scapula in *S. floridanus*. In size and proportions, pelvic girdle, femur, tibiofibula, astragalus, calcaneum, and metatarsals essentially as in *S. floridanus*.

COMPARISONS WITH OTHER SPECIES

From *Hypolagus regalis*, *H. vetus* differs in: P_3 slightly smaller, thick enamel on anterior edge of posteroexternal reentrant from sigmoid to straight, and reentrant projects posteriad (Hibbard, 1969).

From *H. furlongi*, *H. limnetus*, *H. edensis*, and *H. arizonensis*, *H. vetus* differs in markedly larger size.

In structure of P_3 and P^2 and in proportions of the mandible, *H.* cf. *vetus* from the Hagerman local fauna is indistinguishable from *H. vetus* topotypes and specimens from the Anza-Borrego Desert section. Campbell (1969), on analyzing the postcranial skeleton of the Hagerman specimens, concluded that this species had a locomotion similar to that of *Lepus europaeus*. Gregory (1942:338) tentatively referred specimens from the latest Miocene, Niobrara River Formation to *H. vetus*. This assignment was based on the enamel pattern on P_3. This situation seems akin to that between *Sylvilagus floridanus*, *Lepus americanus*, and other species of *Lepus*, which cannot be distinguished from one another on the basis of enamel patterns on the occlusal surface of P_3s (Fig. 6). *S. floridanus* and *L. americanus*, additionally, cannot be distinguished from one another on the basis of skull proportions. It seems therefore that there may be two ecomorphs in *H. vetus* and possibly two species.

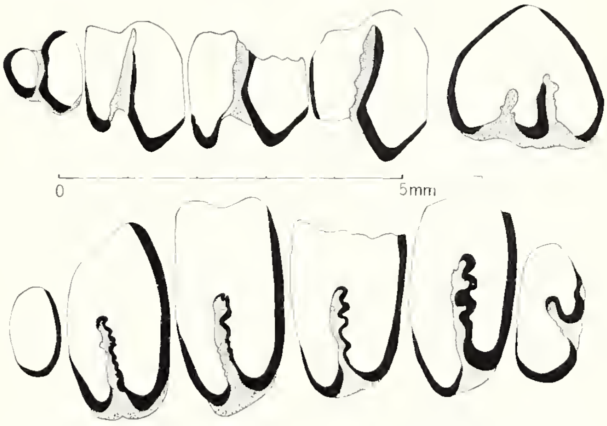

Fig. 8.—Occlusal enamel patterns of *Pewelagus dawsonae* new species: P_3, specimen 13772 from LACM locality 6529; P_4–M_3, specimen 13745 from LACM locality 6540; and upper dentition of specimen 24664 (holotype) from LACM locality 6583.

Pewelagus, new genus

Figs. 7 and 8

Diagnosis.—Near *Sylvilagus bachmani* in size; tympanic bullae larger, both relatively and in actual size, than in any known lagomorph (Table 3). Basicranial-basifacial axis as in *Sylvilagus auduboni*, but with choana narrow as in *Ochotona princeps*.

Age and stratigraphic position.—*Pewelagus* occurs from 488 m (1,601 feet) to 2,407 m (7,920 feet) below top of section. It occurs only in the Blancan part of the section, reaching to the very top of the Blancan (Fig. 4).

The only included species and the type species of the genus is hitherto undescribed and may be called:

Pewelagus dawsonae, new species

Holotype.—LACM 24664, a cranium with left tympanic bulla, zygomatic arches, and anterior end of nasals missing. From LACM locality 6583, Upper Tapiado Wash, Anza-Borrego Desert State Park, San Diego County, California, and 1,526 m (5,020 fect) below top of section, in the Palm Spring Formation.

Referred specimens.—Localities are listed in numerical order and italicized, followed by specimen number.

Locality *1472:* 4467 right mandibular fragment with P_3; 40146 right mandibular fragment with P_3–P_4 and calcaneum; *6529:* 19266 left mandibular fragment with DP_3–DP_4, M_1, 13742 left P_3 and fragments; *6539:* 16833 skull with left mandibular fragment (juvenile); *6540:* 13745 right mandibular fragment with P_4–M_3; *6544:* 23228 rostral fragment with I^1–I^2 and maxillary fragment with P^2–M^3; *6550:* 13744 left mandibular fragment with P_3–M_1; *6552:* 23050 left mandibular fragment with P_3–M_2; *6553:* 23432 left mandibular fragment with P_3–M_1; *6583* (type locality): 39458

Table 3.—*Statistical data relating to* Pewelagus dawsonae *new genus and species from the Anza-Borrego Desert section.*

Measurement	M	N	SD	SE	OR[1]
Anterior surface I^1* to inyon	57.7	1	—	—	—
Anterior surface I^1 to foramen magnum	48.8	1	—	—	—
Anterior surface I^1 to bony palate	17.1	1	—	—	—
L palatine foramen	12.9	1	—	—	—
W palatine foramen	4.3	1	—	—	—
Least APL bony palate	4.5	1	—	—	—
Bony palate to basisphenoid	17.8	1	—	—	—
W choana posterior to bony palate	3.5	1	—	—	—
L basioccipital	10.4	1	—	—	—
APL tympanic bulla	18.8	1	—	—	—
W tympanic bulla	10.1	1	—	—	—
W between bullae	4.0	1	—	—	—
W across occipital condyles	10.0	1	—	—	—
Least postorbital constriction	10.5	1	—	—	—
W across supraorbital ridges	16.4	1	—	—	—
Depth anterior end zygomatic arch	4.2	2	—	—	4.2
W skull anterior end zygomatic arches	24.5	1	—	—	—
Diastema I^2–P^2	14.6	2	—	—	13.7–15.5
L row upper cheek teeth at wear surface	9.2	2	—	—	8.9–9.5
L upper cheek teeth at alveoli	10.4	3	—	—	9.2–11.9
APL I^1	1.2	2	—	—	1.0–1.4
W I^1	1.9	2	—	—	1.7–2.1
W I^2	1.35	2	—	—	1.2–1.5
APL P_3	2.19	11	.26	.08	1.8–2.6
W P_3	1.96	11	.31	.09	1.8–2.7
Diastema I_1–P_3	12.1	1	—	—	—
L row lower cheek teeth at wear surface	9.4	1	—	—	—
L row lower cheek teeth at alveoli	11.85	2	—	—	11.2–12.5

[1] Abbreviations as explained [or, of words in the same places] in Table 2.
* Abbreviations as explained in Table 1.

skeletal fragments, left maxillary with P^2–M^2, right maxillary fragment with P^3–M^2, mandibular fragment with P_3–M_1, proximal epiphysis of tibia, fragment of right innominate, 23439 left mandibular fragment with P_3, 13728 right mandibular fragment with P_3–M_2; *6604:* 17650 fragmentary cranium; *6642:* 19562 left P_3; *6722:* 17671 skull with right mandible (juvenile); *6811:* 24970 left mandibular fragment with P_3–M_2; *6821:* 23174 right P_3.

IVCM: locality *27:* 308 right mandibular fragment with P_3.

Diagnosis.—Same as for genus.

Etymology.—From *pewe,* Algonquin for small, and *lagus,* Greek for hare. Named for Mary R. Dawson, for her outstanding work on lagomorphs.

Description

Skull.—Tympanic bullae relatively large and laterally compressed; their posterior ends extend slightly posteriad of occipital condyles separating paroccipital process from squamosal process of squamosal; anterior ends extend almost into pterygoid fossae. Wall of bulla simple, without sponge-like structures present in *Scalopus, Ochotona, Perognathus, Thomomys, Geomys,* and *Mustela,* and without mastoid portion delimited by a septum as in *Dipodomys.* Basisphenoids and basioccipitals constricted between bullae, the suture between them posteriad of anterior end of bullae. Most of left bulla missing in holotype but entotympanic present and sutured to basioccipital and posterior portion of basisphenoid. Immediately posterior to level of cavernous foramen, entotympanic, following contour of bulla, diverges laterally to basisphenoid, leaving a slit-like opening between the two bones, which is here interpreted as representing the pharyngeal opening of the Eustachian tube. Foramem lacerum situated laterad of anterior end of bullae and medioposteriad of lateral lamina of pterygoid fossa. Orbital fissure and optic foramen as in other leporids, as is anterior half of cranium. Fenestrations on side of rostrum as in other leporids, but those in basicranial region almost absent, probably reflecting the forward extension of bullae, and consequent lateral displacement of foramen lacerum from its normal median position. Interparietal visible; supraorbital processes small as in *Brachylagus.* External

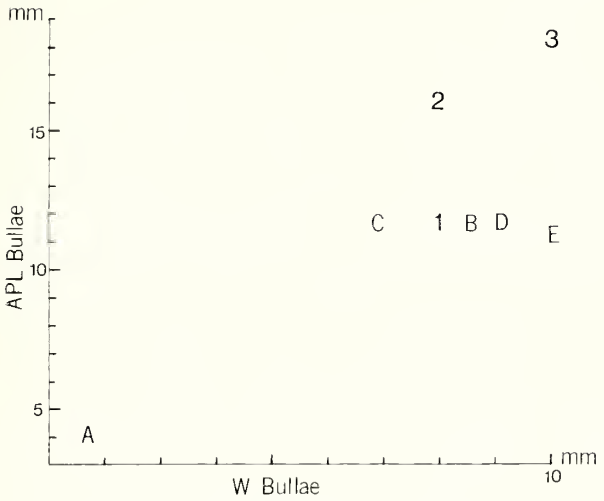

Fig. 9.—Diagram comparing the growth of the tympanic bullae of domesticated *Oryctolagus cuniculus* and *Pewelagus dawsonae* new species. A–D represent juveniles and D an adult *Oryctolagus*. 1 (specimen 16833), and 2 (specimen 17671) are juveniles, and 3 (holotype) is an adult of *Pewelagus dawsonae*. See text for further details.

auditory meatus enlarged and directed dorsoposteriad. Palatal bridge extends from middle of M^1 to middle of P^2.

The "pistol grip"-like flexion of the posterior end of skull, as expressed by the basicranial-basifacial axis and doming of parietals, is nearest *Sylvilagus auduboni*, and far greater than in *Romerolagus*, *Palaeolagus hypsodus*, and *Ochotona*.

Dentition.—P^2, essentially as in *Brachylagus*, ovoid in cross section with a deep anterior reentrant inflected at the medial half, which extends posterolabiad. A shallow reentrant sometimes present in labial one-third of tooth. Hypostriae on P^3–M^2 have crenulations on anterior enamel that become reduced toward back of tooth rows. Crenulations on posterior enamel of hypostriae almost absent. M^3 roughly oblong in cross section with thick enamel only on anterior and anterolabial sides of tooth.

P_3 typically archaeolagine in enamel pattern, posterior external reentrant extending almost half way across crown; anteroexternal reentrant extends slightly less than one-third the way across the tooth, and has one or two crenulations. P_4–M_3 essentially as in *Hypolagus*.

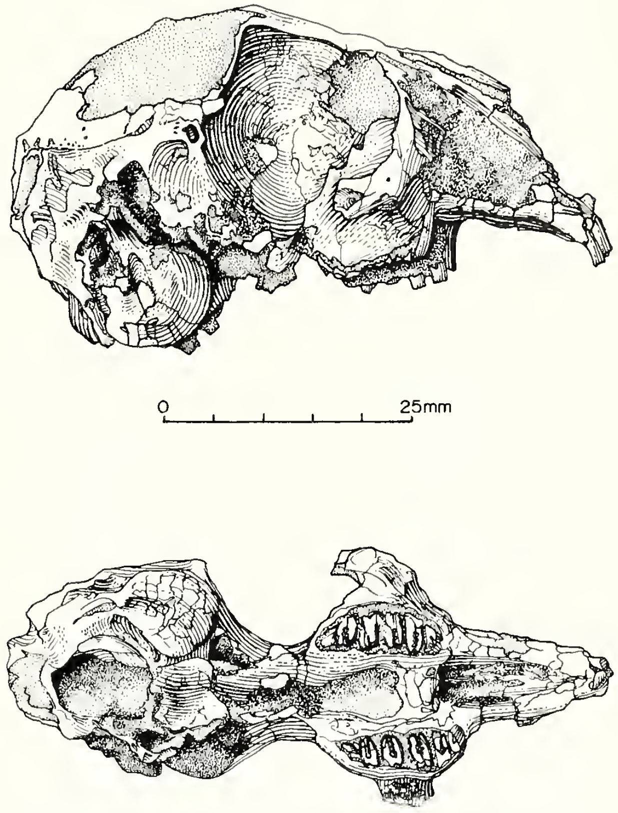

Fig. 10.—Right-lateral and ventral views of the cranium of *Nekrolagus* species, specimen 24958 from LACM locality 6604. Drawn by Erica H. Craig.

Development of tympanic bullae.—Specimens 16833 and 17671 are juveniles. For comparisons, four litter mates of domesticated *Oryctolagus cuniculus* were sacrificed, respectively, starting 10 days after birth and at 10 day intervals to the 40th day (Fig. 9, A–D), and the skulls were cleaned. The skull of an adult individual was added to the series (Fig. 9, E). *Pewelagus* specimen 16833 corresponds in tooth development and suture closure to *Oryctolagus* stage D, whereas specimen 17671 corresponds to stage E (Fig. 9, 1–2). The *Pewelagus* holotype is an adult (Fig. 9, 3).

The development of the tympanic bullae in *Pewelagus* differs markedly from that in *Oryctolagus*. In *Oryctolagus* the anteroposterior length (APL) is attained by the 20th day of life, while in *Pewelagus* the full APL is not attained until much later (Fig. 9).

Comparisons With Species of Other Genera

The P_3 in *P. dawsonae* is characteristic for the archaeolagines and is here briefly compared with P_3s in species of *Hypolagus*.

The small P_3 in *P. dawsonae* distinguishes this species from *H. vetus* Dice (1917), *H. regalis* Hibbard (1939), and *H. oregonesis* Shotwell (1956).

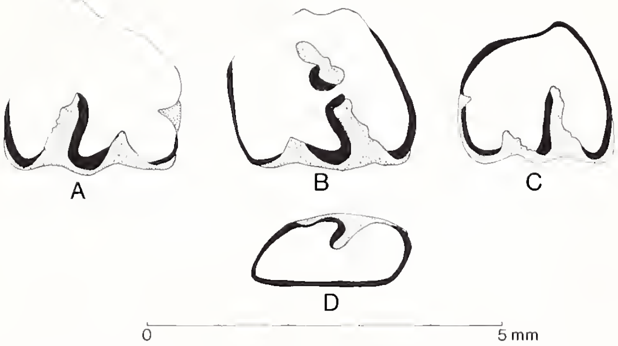

Fig. 11.—Right and left P_3s (A and B) and right P^2 (D) occlusal patterns of *Nekrolagus* species, specimen 24958 from LACM locality 6604; and left P_3 (C) of ?*Nekrolagus* species, specimen 7005 from LACM locality 1711.

Crenulations in the anteroexternal reentrant set *P. dawsonae* apart from *H. furlongi* Gazin (1934). The anteroexternal reentrant is relatively shallower than in *H. limnetus* Gazin (1934) and *H. fontinalis* Dawson (1958). In *H. arizonensis* Downey (1962) the posteroexternal reentrant turns sharply posteriad whereas in *P. dawsonae* it is straight.

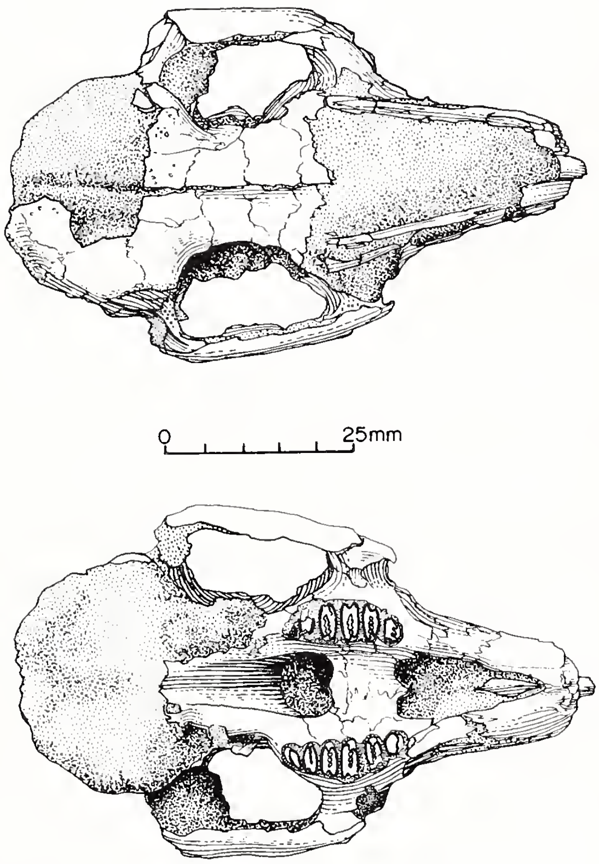

Fig. 12.—Dorsal and ventral views of the cranium of *Sylvilagus hibbardi* new species, specimen 3479 from LACM locality 1301. In this specimen the zygomatic arches are plastic and contain impressions of the medial surfaces of the arches. Drawn by Erica H. Craig.

The P_3 in *H. edensis* Frick (1921) has a size and pattern comparable to that in *P. dawsonae* and may be referable to this genus. Because *H. edensis* is known only from the holotype, this relationship can be better determined with additional specimens.

Subfamily Leporinae Trouessart 1880

Genus ***Nekrolagus*** Hibbard 1939

***Nekrolagus* species**

A skull, LACM 24958 (Fig. 10), was obtained from locality LACM 6604, which is 2,140 m (7,020 feet) below top of section, in the Early Blancan of the Palm Spring Formation (Fig. 4). The specimen is that of a juvenile, approximately the size of and having the same basicranial-basifacial flexion as *Sylvilagus nuttallii*. It is remarkably similar to the latter species in skull proportions and thus referable to the cottontail ecomorph.

P^2 has a deep anterior reentrant and a shallower reentrant between the lingual edge of the tooth and the deep reentrant (Fig. 11). The thin enamel on the posterior edge of the hypoflexus in P^3–M^2 has few crenulations.

An enamel lake extends to the base of the crown on left P_3 with no trace of an anterior reentrant, whereas on the right P_3 there is an anterior reentrant but no trace of an enamel lake (Fig. 11, A and B).

The juvenile nature of this specimen coupled with the variation, especially in the P_3s, precludes assigning it to a species of *Nekrolagus*.

?*Nekrolagus* species

A left mandible, LACM 7005, with complete dentition and from LACM locality 1711, is of a juvenile individual (Fig. 11, C). In this specimen there is an anterior reentrant on P_3, but the configuration of the posteroexternal reentrant differs from *Nekrolagus* and other leporids from this geologic section, juveniles or adults. The specimen, furthermore, lacks an enamel lake on P_3. The posteroexternal reentrant on P_3 resembles that for *Nekrolagus* figured in Hibbard (1963: fig. 1f).

Genus ***Sylvilagus*** Gray 1867

Sylvilagus hibbardi, new species

Figs. 6,12,13

Holotype.—LACM 4394 from LACM locality 1615, mandibular fragment with P_3–M_3.

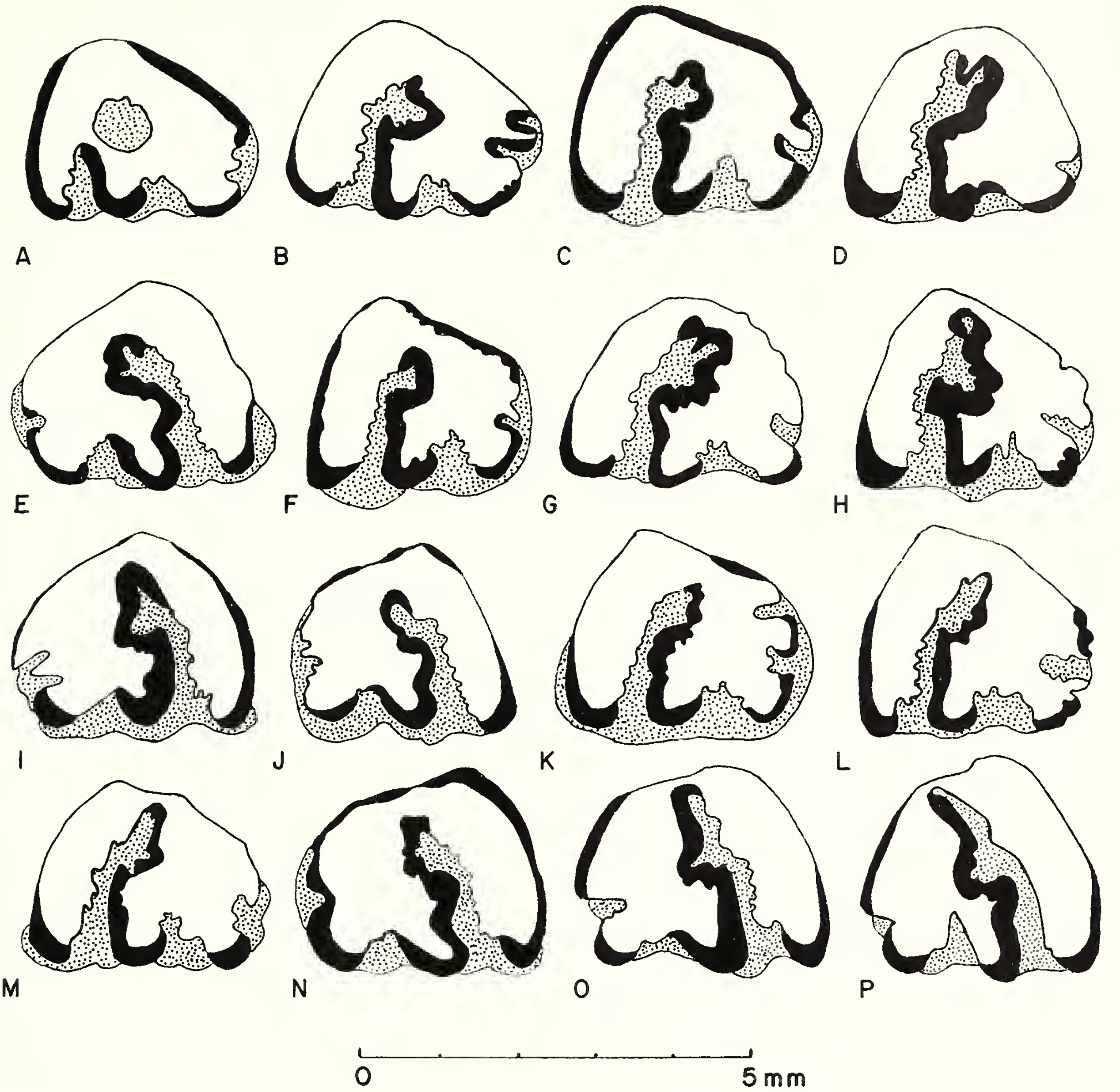

Fig. 13.—Enamel patterns on the occlusal surfaces of P_3s in *Sylvilagus hibbardi* new species, showing a morphological series from A (*Nekrolagus* pattern) to P (*Lepus* pattern). This series is independent of stratigraphic relationships. The numbers of the figured specimens (LACM) are listed in the same order as above (A to P): 23224, 4430, 24963, 24983, 24959, 24962, 4406, 6930, 24978, 24960, 24964, 4426, 24984, 24961, 4425, and 24982.

Diagnosis.—Approximately the size of *Hypolagus vetus* and *Sylvilagus floridanus* (Table 4). P_3 with a predominant pro-*Sylvilagus* enamel pattern, and usually with two or more anterior reentrants.

Age and stratigraphic position.—*S. hibbardi* occurs from 152 m (500 feet) to 1,042 m (3,420 feet) below top of section, and from Late Blancan to Irvingtonian, in the Palm Spring Formation (Fig. 4).

Referred specimens.—Localities are listed in numerical order and italicized, followed by specimen numbers.

Locality *1112:* 3329 left mandibular fragment with P_3–M_2; *1114:* 3330 left P_3, 3331 right P_3, 24975–24977 left P_3s, 24978–24982 left P_3s, 24983–24986 right P_3s, 24987–24988 left P^2s, 24989–24991 right P^2s, 24992 left P_3, 24993 left P^2, 3695 left mandibular fragment with P_3–M_2, 3696 right mandibular fragment with P_3–P_4, 4455 left P^2, 4460 one left and one right P_3, 20206 left P_3; *1196:* 23225 two left P_3s; *1245:* 4425 left man-

Table 4.—*Statistical data relating to* Sylvilagus hibbardi *new species from the Anza-Borrego Desert section.*

Measurement	M	N	SD	SE	OR[1]
L palatine foramen*	18.2	2	—	—	18.0–18.4
W palatine foramen	8.5	1	—	—	—
Least APL bony palate	6.4	6	3.67	1.64	5.9–7.2
Bony palate to basisphenoid	22.1	—	—	—	—
W choana posterior to bony palate	6.1	2	—	—	5.4–6.8
Least postorbital constriction	14.0	3	—	—	12.9–16.0
Depth anterior end zygomatic arch	5.9	6	.42	.19	5.1–7.5
W skull anterior end zygomatic arches	32.2	2	—	—	31.4–33.0
Diastema I^2–P^2	19.1	1	—	—	—
L row upper cheek teeth at wear surface	12.2	3	—	—	11.5–12.7
L row upper cheek teeth at alveoli	14.2	5	.83	.41	13.6–14.7
W I^1	2.5	1	—	—	—
W I^2	1.2	1	—	—	—
APL P_3	2.9	40	.034	.005	2.5–3.4
W P_3	2.4	41	.179	.028	2.0–2.7
Diastema I_1–P_3	16.3	1	—	—	—
L row lower cheek teeth at alveoli	13.5	6	.75	.34	12.5–14.4

[1] As in Table 2.

* Abbreviations as explained in Table 1.

dibular fragment with P_3–M_2; *1249:* 3337 left mandibular fragment with P_4–M_3; *1301:* fragmentary cranium with basicranium missing; *1357:* 23057 left P_3; *1358:* 17624 right P^2; *1428:* 23227 one left and one right P_3; *1466:* 6930 right P_3; *1469:* 6760 left mandibular fragment with P_3–M_2; *1472:* 4467 right mandibular fragment with P_3–M_1; *1513:* 4426 right mandibular fragment with P_3–M_3; *1586:* 4430 right mandibular fragment with P_3–M_1; *1588:* 4429 two palates with P^2–M^3 on each side, and right mandibular fragment with P_3–M_3, 6949 right P_3; *1606:* 7951 right mandibular fragment with P_3–M_3; *1615* (type locality): 4395 right mandibular fragment with P_3–M_2, 23172 left mandibular fragment with P_3–M_2, 24959–24961 left P_3s, 24962–24964 right P_3s; *3235:* 40142 left mandibular fragment with P_3–M_1; *65183:* 23224 skull fragment with dentitions; *6642:* 19562 left P_3; *66114:* 17201 right mandibular fragment with P_3–M_1.

IVCM: locality *82:* 329 left mandibular fragment with P_3–M_3; *292:* 1143 cranial fragment with rostrum and braincase missing; *396:* 1475 right mandibular fragment with P_3–M_3.

Etymology.—Named for the late Claude W. Hibbard in recognition of his contribution to our knowledge of evolution in Late Cenozoic leporids.

DESCRIPTION

In size and proportions of skull, this species resembles *Sylvilagus floridanus.* Interparietal visible in specimen IVCM 143, and wavy sutural contact between parietal and interparietal can be seen in specimen LACM 3479.

In specimen LACM 3479, a rugose patch four mm long is present on anterior part of ridge marking dorsal margin of origin of temporal muscle, and on sutural contact between squamosal and parietal. This rugose patch probably represents the area of attachment (ankylosis) of postorbital process to braincase. This attachment is found in some species of *Sylvilagus,* and although postorbital process may touch braincase in *Lepus,* there is never a broad area of attachment in the latter genus (Nelson, 1909:40).

In *S. hibbardi,* 57% of the P_3s have the "pro-*Sylvilagus,*" 39% the "*Lepus,*" 2% the "*Nekrolagus,*" and 2% the "paedomorphic" patterns of enamel on the occlusal surface (Hibbard, 1963). Although Hibbard (1963) did not define the pro-*Sylvilagus* enamel pattern in that paper, he wrote to me in 1969: "[Do] you consider the 'prosylvilagus' pattern the one where it clearly shows the joining of the posteroexternal reentrant [on P_3] with the enamel island instead of the more typical straight reentrant? If that is what you call the prosylvilagus pattern it is what I saw in *Lepus* and *Sylvilagus* when it was determined that *Nekrolagus* gave rise to the Recent [*Lepus*] pattern." In Fig. 13 is a morphological series of P_3s showing the transition from *Nekrolagus* to the *Lepus* pattern.

P^2s have three anterior reentrants, normal for other species of *Sylvilagus.*

COMPARISONS WITH OTHER SPECIES

Sylvilagus hibbardi is comparable in size to *S. auduboni, S. floridanus, S. braziliensis,* and *S. graysoni;* smaller than *S. aquaticus* and *S.* cunicularius; and larger than *S. bachmani, S. insonus, S. leonensis, S. nuttallii, S. palustris,* and *S. transitionalis.* It differs from all known species of *Sylvilagus* in the predominant pattern of the enamel on P_3.

Ecological Replacement

Presumably *Hypolagus vetus* is ecologically replaced by *Sylvilagus hibbardi* in the Anza-Borrego

Desert section (Fig. 4). In size and in proportions of the skull these two species are almost identical. If so, this is a case of a leporid of one ecomorph being replaced by another leporid of a different subfamily but of the same ecomorph. The paleoclimate in the Anza-Borrego Desert section, especially in that part of the section where the above ecological replacement occurs, remained essentially unchanged, judging from the lack of observed change in the sediments and faunal elements in that part of the section (Woodard, 1963; Downs and White, 1968).

Pewelagus dawsonae was contemporaneous with *Hypolagus vetus* and *Sylvilagus hibbardi* in the Anza-Borrego Desert section and it is doubtful that it became extinct as a result of competition with the other leporids known to occur in the section. *P. dawsonae* is highly specialized and falls outside the heretofore known ecological "spectrum" of lagomorphs.

Leporinae, genus and species indeterminate

Three mandibular fragments of an advanced leporine were obtained from the latest Blancan (IVCM locality *113*, specimens 413 and 1275) to late Irvingtonian (LACM locality 1906, specimen 24889) part of the section (Fig. 4). These specimens are large, comparable to the mandibles in *Lepus townsendii* and *Sylvilagus cunicularius* (Fig. 6). In enamel patterns of cheek teeth, specimens of *S. cunicularius* are indistinguishable from any North American species of *Lepus* or *Sylvilagus*. Thus, if the only available characters to identify a specimen are size and enamel patterns on P_3, the specimen cannot be referred with certainty to either *Lepus* or *Sylvilagus*.

MORPHO-ECOLOGICAL RELATIONSHIPS

As shown by White and Keller (1983), the living species of North American lagomorphs fall into three ecomorphs: "jack rabbit," "cottontail," and "rock rabbit." These ecomorphs are based on the correlation of proportions of the skull with ecology. Using the information from living lagomorphs and known proportions of extinct forms, one can infer ecomorphs for the latter.

Hypolagus vetus from the Anza-Borrego Desert section seems referable to the cottontail ecomorph (Figs. 5 and 14). Dawson (1958) suggested, based on her analysis of known characters of *Hypolagus vetus* from Thousand Creek, Nevada, that *H. vetus* was less cursoreal than *Sylvilagus*, but closer in mode of locomotion to *Sylvilagus* than to *Romerolagus*. From measurements made on fragmentary mandibles and maxillaries in this study, *H. vetus* from Thousand Creek seems to be referable to the cottontail ecomorph.

If Campbell's (1969) analysis of the limb bones of *Hypolagus* cf. *H. vetus* from Hagerman indicate locomotion as in *Lepus europaeus*, then the species from Hagerman is referable to the jack rabbit ecomorph.

From the foregoing, it seems that within the genus *Hypolagus* there is a cottontail and a jack rabbit ecomorph.

Among the living species of North American *Lepus* (Figs. 5 and 14), *L. americanus* is "ecomorphically" a cottontail, whereas *L. arcticus*, *L. californicus*, and *L. townsendii* are jack rabbits (White and Keller, 1983). Enamel patterns on P^2 and P_3 cannot be used to distinguish between *Lepus* and *Sylvilagus* or between species of *Lepus*. *Lepus* and *Sylvilagus* can be distinguished from one another by the presence or absence of a visible interparietal, altricial (*Sylvilagus*) *versus* precocial (*Lepus*) young (Hall and Kelson, 1959:246), and by the electrophoretic patterns of hemoglobin (Johnson, 1968). With fossils, it seems probable that taxonomic decisions, in some cases, will be difficult if not impossible. Black (1963), for example, referred all fossil chipmunks to *Tamias* when it became evident that *Tamias* and *Eutamias* could not be distinguished from one another on the basis of available dental and skeletal structures. He stated, "The material . . . has been placed in *Tamias* as a purely arbitrary assignment" (Black, 1963:129). White (1953) thought that chipmunks probably did not constitute a natural (phylogenetic) group. *Tamias* and *Eutamias*, and probably other groups of small squirrels, can be referred to a chipmunk ecomorph.

Pewelagus dawsonae.—The structure of the cranium in *P. dawsonae* suggests an erect posture similar to that in *Sylvilagus* and *Brachylagus*. This is based primarily on a pistol grip-like flexion of the posterior end of the cranium.

The choanae in *Ochotona*, *Pewelagus*, and *Palaeolagus hypsodus* are relatively narrow, intermediate in cottontails, and broadest in jack rabbits (Fig. 5). The relative width of the choana seems to cor-

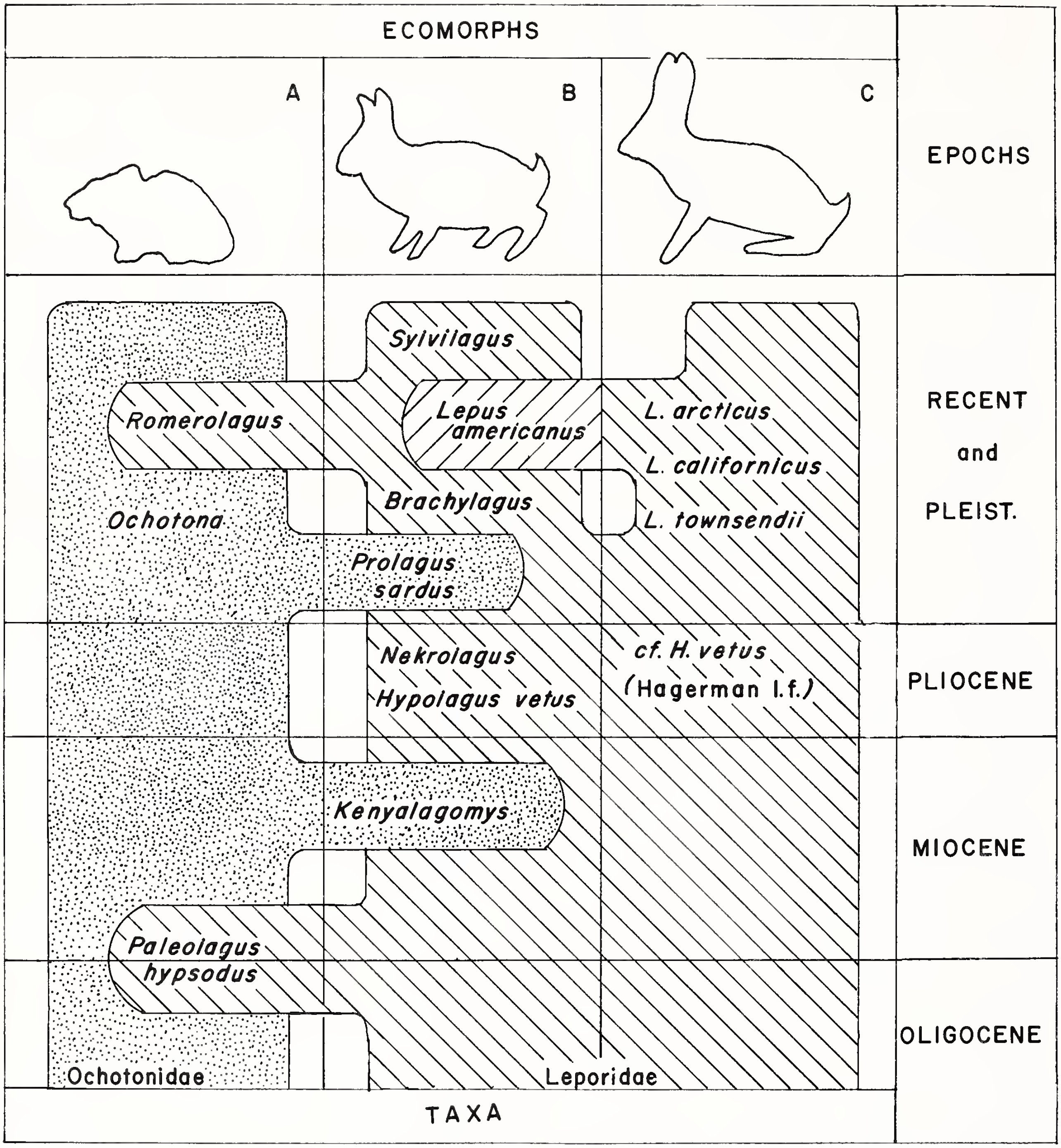

Fig. 14.—Diagram summarizing the distinction between taxa and ecomorphs. Modified from White and Keller (1984). The ecomorphs are: A, rock rabbit; B, cottontail; and C, jack rabbit.

relate broadly with the degree to which a species lives in a sheltered environment. Most burrowing forms tend to have relatively narrow choanae.

The relative width of choanae also may correlate with the degree to which animals do sustained running (Dawson, 1958). Jack rabbits escape their enemies by swift and sustained running, cottontails less so, and rock rabbits least of all.

The flexion of the posterior end of the cranium, the greatly enlarged tympanic bullae, and narrow choanae suggest that *P. dawsonae* lived in burrows and escaped snakes and owls in a manner similar to *Dipodomys* (Webster, 1962). The aberrant morphology of this genus precludes referring it to any known ecomorph.

Palaeolagus hypsodus.—*P. hypsodus* from the Early Miocene is clearly a leporid, yet in proportions of the skull it resembles *Ochotona.* When measurements of the skull in *P. hypsodus* and *O. alpina* from the Soviet Union are compared, striking similarities are noted (Table 5). The latter measurements, together with the lack of flexion of the posterior end of the skull and the ochotonid-like postcranial skeleton in *P. hypsodus* (Dawson, 1958), strongly suggest that this species belongs with the rock rabbit ecomorph.

Prolagus sardus.—*P. sardus* is clearly an ochotonid but has some characters that are found in leporids. Dawson (1969:184) wrote: "In the skull the basicranial-basifacial bending indicates that the head was held somewhat more upright than in *Ochotona,* though less so than in *Romerolagus.*" She further stated (p. 187) that "The range of movements was probably more comparable to that in Oligocene leporids such as *Palaeolagus* and *Megalagus.*" It would seem that *P. sardus* trends toward a cottontail ecomorph to the same degree that *Romerolagus* (White and Keller, 1983) trends toward the rock rabbit ecomorph.

Kenyalagomys.—MacInnes (1953:20) points out that in this ochotonid there are some features that show striking affinities to the leporids. These features are: degree of maxillary fenestration, invasion of the dorsal surface of the skull by the supraoccipital, high occiput, apparent separation of the lachrymal and orbito-sphenoid by a process from the maxilla and not one from the frontal, form of the coronoid process and the anterior wall of the ascending ramus, and the size and shape of the masseteric fossa. Based on the foregoing, I consider *Kenyalagomys* referable to the cottontail ecomorph.

Table 5.—*Cranial measurements in mm of* Ochotona alpina *and* Palaeolagus hypsodus.

Measurements	*O. alpina*	*P. hypsodus*
Greatest length of skull	54.2	54.8
Width of choanae	2.7	2.2
APL tympanic bullae	15.8	16.0
W tympanic bullae	11.2	10.7
Zygomatic breadth	22.5	22.3
L upper diastema I^2–P^2	11.9	11.5

* Abbreviations as explained in Table 1.

Romerolagus diazi.—This living species of leporid is morphologically, ecologically, and behaviorally similar to *Ochotona* (White and Keller, 1984). It can easily be referred to the rock rabbit ecomorph, yet in the enamel patterns of the cheek teeth, and in other features of the skull, *R. diazi* is clearly a leporid.

Nekrolagus species.—The striking similarity between this specimen (LACM 24958), the only known skull of this genus, and *Sylvilagus nuttallii* strongly suggests it to be referable to the cottontail ecomorph. Its smaller size compared to *H. vetus* suggests the two species occupied different ecological niches.

DISCUSSION

Wood (1940), from what was known of pertinent skeletons at that time, considered *Palaeolagus* to be at approximately the same stage of locomotive development as *Ochotona,* and *Megalagus* to have been near the same stage as *Sylvilagus.* The latter seems to be comfirmed by the relative size of the choana (LACM no.: C.I.T.1563) of *Megalagus turgidus* (Dawson, 1958: figs. 1–6). Thus, morpho-ecological diversity probably existed in leporids in the Oligocene.

Romerolagus is clearly a leporid, yet its skull proportions and habits tend to resemble those in ochotonids. Taxonomically, *Lepus americanus* is indeed a species of *Lepus,* while at the same time its skull proportions and habits are as in *Sylvilagus.* Hence, functionally, *L. americanus* is a cottontail and not a jack rabbit (White and Keller, 1984).

White and Keller (1984) wrote that: ". . . some osteological characters imply a common ancestry whereas others correlate with habits, and are the result of convergence. A distinction needs to be made between a taxon and an ecomorph. This distinction is seldom clear since it involves dealing with the interaction between selective forces and phenotypes (ultimately genotypes) through a spectrum of structural and functional variations, and only characters which are near each end of the spectrum can provide distinctions. Thus in lagomorphs, characters resulting presumably from similar selective pressures are identified by their functions or presumed functions with respect to habits and other ecological factors. Some such characters are: 1. width of choanae; 2. degree of development of supraorbital ridges; 3. posture, as implied by the flexion of the basicranial-basifacial axis; 4. relative length of hind foot; and 5. length of upper and lower diastemata between incisors and cheek teeth.

At the other end of the above spectrum, characters that are presumed to be 'independent' of any apparent selective forces, and on which most systematic decisions are based, are as follows in lagomorphs: 1. enamel tooth patterns; 2. hypsodonty and degree of rooting in cheek teeth; 3. altricial *versus* precocial young; and 4. electrophoretic patterns of hemoglobin."

From the foregoing it seems likely that the rock rabbit and cottontail ecomorphs were already established by the Oligocene and the jack rabbit ecomorph by Pliocene times. If the latter is true, then one might ask, what osteological characters in ochotonids or leporids might be considered to have resulted from a common ancestry, or what characters indicate ecological relationships?

Dawson (1969) stated that a primitive lagomorph would not be completely *Ochotona*-like but would have features now associated with living Leporidae and lost in the Ochotonidae.

As indicated by discussions of Dawson (1958 and 1969), Wood (1957), and MacInnes (1953), it is evident that distinguishing ochotonids from leporids by osteology is less feasible than by patterns of dentition. This may very well be related to gradations of ecomorphic relationships or of osteological features related to adaptation and not necessarily to common ancestry. It would seem, therefore, that no known lagomorph can be considered to be ancestral to all lagomorphs.

LITERATURE CITED

Black, C. C. 1963. A review of the North American Tertiary Sciuridae. Bull. Mus. Comp. Zool., Harvard Univ., 130:109–248.

Berggren, W. A., and J. A. Vancouvering. 1974. The Late Neogene: biostratigraphy and paleoclimatology of the last 15 million years in marine and continental sequences. Palaeogeogr., Palaeoclimatol., Palaeoecol., 16:1–216.

Brandt, J. F. 1855. Beitrage zur nahern Kenntniss der Saugethiere Russlands. Mem. Acad. Imp. Sci. St. Petersbourg, ser. 6, 9:1–375.

Campbell, K. E., Jr. 1969. Comparing postcranial skeletons of Pliocene rabbits. Michigan Academician, Papers Michigan Acad. Sci. Arts, and Letters, 1:99–115.

Craigie, E. H. 1948. Bensley's practical anatomy of the rabbit. 8th ed., Univ. Toronto Press, Toronto, 1–391.

Dawson, M. R. 1958. Late Tertiary Leporidae of North America. Univ. Kansas Paleont. Contrib., Vertebrata, 6:1–75.

———. 1969. Osteology of *Prolagus sardus*, a Quaternary ochotonid (Mammalia, Lagomorpha). Palaeovertebrata, 2:157–191.

Dibblee, T. W., Jr. 1954. Geology of the Imperial Valley region, California. Chapter 2 (pp. 21–28) *in* Geology of the natural provinces. Geol. Southern California, Division of Mines, State of California. Bull. 170, 160 pp.

Dice, L. R. 1917. Systematic position of several American Tertiary lagomorphs. Univ. California Publ., Bull. Dept. Geol., 10:179–183.

Downey, J. S. 1962. Leporidae of the Tusker local fauna from southeastern Arizona. J. Paleont., 36:1112–1115.

Downs, T., and J. A. White. 1968. A vertebrate faunal succession in superposed sediments from Late Pliocene to Middle Pleistocene in California. Proc. 23rd. Internat. Geol. Congr., 10:41–47.

Frick, C. 1921. Extinct vertebrate faunas of the badlands of Bautista Creek and San Timoteo Canyon, southern California. Univ. California Publ., Bull. Dept. Geol., 12:277–424.

Gazin, C. L. 1934. Fossil hares from the late Pliocene of southern Idaho. Proc. U.S. Nat. Mus., 83:111–121.

Gregory, J. T. 1942. Pliocene vertebrates from Big Spring Canyon, South Dakota. Univ. California Publ., Bull. Dept. Geol., 26:307–446.

Gray, J. E. 1821. On the natural arrangement of vertebrose animals. London Medical Repository, 15:296–310.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Ronald Press, New York, 546 pp.

Hibbard, C. W. 1939. Four new rabbits from the upper Pliocene of Kansas. Amer. Mid. Nat., 21:506–513.

———. 1963. The origin of the P_3 pattern of *Sylvilagus, Caprolagus, Oryctolagus,* and *Lepus.* J. Mamm., 44:1–15.

———. 1969. The rabbits (*Hypolagus* and *Pratilepus*) from the Upper Pliocene, Hagerman local fauna of Idaho. Michigan Academician, Papers Michigan Acad. Sci. Arts, and Letters, 1:81–97.

Johnson, M. L. 1968. Application of blood protein electrophoretic studies to problems in mammalian taxonomy. Syst. Zool., 17:23–30.

MacInnes, D. G. 1953. The Miocene and Pleistocene Lagomorpha of East Africa. Brit. Mus. (Nat. Hist.) Fossil Mamm. Africa, 6:1–30.

Marshall, L. G., R. F. Butler, R. E. Drake, G. H. Curtis, and R. H. Tedford. 1979. Calibration of the Great American Interchange. Science, 204:272–279.

Nelson, E. W. 1909. The rabbits of North America. North American Fauna no. 29:1–314.

Opdyke, N. D., E. H. Lindsay, N. M. Johnson, and T. Downs. 1977. The paleomagnetism and magnetic polarity stratigraphy of the mammal-bearing section of Anza-Borrego State Park, California. Quat. Res., 7:316–329.

Shotwell, J. A. 1956. Hemphillian mammalian assemblage from northeastern Oregon. Bull. Geol. Soc. Amer., 67:717–738.

Simpson, G. G., A. Roe, and R. C. Lewontin. 1960. Quantitative Zoology. (Rev. Ed.) New York, Harcourt, Brace and Co., 440 pp.

Webster, D. B. 1962. A function of the enlarged middle-ear cavities of the kangaroo rat, *Dipodomys.* Physiol. Zool., 35: 248–255.

White, J. A. 1953. Genera and subgenera of chipmunks. Univ. Kansas Publ., Mus. Nat. Hist., 5:543–561.

White, J. A., and B. L. Keller. 1984. Morphological stability and morpho-ecological relationships in North American Lagomorpha. Spec. Publ., Carnegie Mus. Nat. Hist., 9:58–66.

Wood, A. E. 1940. The mammalian fauna of the White River Oligocene. Part III, Lagomorpha. W. B. Scott and G. L. Jepsen, eds., Trans. Amer. Phil. Soc. new ser., 28:269–362.

———. 1957. What, if anything, is a rabbit? Evolution, 11: 417–425.

Woodard, G. D. 1963. The Cenozoic stratigraphy of the western Colorado Desert, San Diego and Imperial Counties, Southern California. Unpublished Ph.D. thesis, Univ. California, Berkeley.

Woodring, W. P. 1931. Distribution and age of the Tertiary deposits of the Colorado Desert. Carnegie Inst. Washington Publ. 148:1–25.

Address: Idaho Museum of Natural History, Pocatello, Idaho 83209.

EVOLUTIONARY STABILITY AND ECOLOGICAL RELATIONSHIPS OF MORPHOLOGY IN NORTH AMERICAN LAGOMORPHA

John A. White and Barry L. Keller

ABSTRACT

Mastication in lagomorphs probably has remained essentially unchanged since the Late Eocene and may have contributed to the morphological stability of the order by profoundly affecting the shape of the skull. Analysis of 31 measurements of 11 species (341 means) represented by 211 skulls of leporids and ochotonids reveals that the North American Lagomorpha fall into three ecomorphs irrespective of taxonomic relationships. The ecomorphs are jack rabbit, cottontail, and rock rabbit. The term ecomorph is proposed to include organisms whose morphological resemblances resulted from convergence owing to ecological preference. Cluster analysis failed to differentiate between quantitative morphological characters that are ecomorphic from those resulting from a common ancestry.

INTRODUCTION

Students of the Order Lagomorpha have long postulated that hares, rabbits, and pikas are characterized by evolutionary stability in morphology (Dawson, 1958; Wood, 1957). This stability is reflected in the taxonomic characters employed in classifying the various species of the order, such as presence or absence of a visible interparietal bone, altricial versus precocial young, and enamel patterns on the cheek teeth.

Hall and Kelson (1959:246) stated: "Correlation of structure with function is well illustrated among the lagomorphs by means employed by the different species to detect and escape from their enemies. A gradient series is evident in which the pikas and jack rabbits are the extremes."

Here we attempt to quantify the correlation of structure and function with analyses of skull measurements and, in turn, to relate these to broad ecological "preferences" in lagomorphs. Furthermore, we suggest that the functional anatomy of the chewing apparatus, as implied from scratches on the enamel of occlusal surfaces of cheek teeth, is related to the evolutionary stability postulated to exist in this order.

Special editor's note.—This is the same paper as that cited (under date of 1981) by J. J. Becker and J. A. White and by the title "Morpho-evolutionary stability and morphoecological relationships in North American Lagomorpha" (J. Vert. Paleont., 1:218, September 1981.

MATERIALS AND METHODS

Cranial Comparisons

All measurements were made with dial calipers calibrated to 0.1 mm. All anatomical terminology is that of Craigie (1948).

Thirty-one measurements were made in each of 211 skulls which are listed by taxon, museum acronym (see acknowledgments), and catalog numbers, as follows: *Ochotona princeps,* UMZM, 589, 3916, 6378, 8174–8177, 8322, 8336, 8355, 8550, 8551, 8985, 15201, 15203, 15217, 15218, 15229; IMNH, 7009. *Romerlagus diazi,* AMNH, 146939, 148172–148178, 148180, 148181; USNM, 57954, 174531, 174533, 174534. *Brachylagus idahoensis,* USNM, 23104, 30960, 31463, 54511, 54798, 80231, 170030, 231440, 236412, 243294, 264350. *Sylvilagus auduboni,* USNM 44662, 58042, 64484, 64485, 133354, 133402, 133403, 146527–146532, 147916, 150438, 160122, 160493, 189203, 214126, 263051. *S. cunicularius,* AMNH, 23962–23964, 23967–23969, 23972, 23973, 23975–23978, 24691–24698; MDZA, 15133. *S. floridanus,* USNM, 24118, 64035, 64036, 64042, 64049, 64051, 64052, 70900, 76711, 77114, 78754–78756, 80334, 189135, 189137, 232023, 245787, 264715, 264717. *S. nuttallii,* USNM, 31112, 31114, 31395, 67873, 67875, 74376, 74832, 79278, 79279, 79367, 80184, 80186, 95556, 168341, 168350, 168502, 169591, 170029, 234186, 276001. *Lepus americanus,* USNM, 23123, 56005–56007, 68710, 73697, 73698, 106861, 116267, 129686, 170767, 180168, 189037, 189040, 189042, 189044, 189126, 245881, 257457, 287625. *L. arcticus,* USNM, 7203, 23121, 23129, 23130, 23133, 78125, 78126, 114850, 114855, 114861, 126170, 126171, 189017, 245938, 245954, 245955, 248724, 248725, 248729, 276620. *L. californicus,* USNM, 3226, 23483, 23484, 43724, 43725, 44069, 44071, 44380, 55314, 55315, 58041, 63850–63852, 64289–64291, 64472, 64473, 64490. *L. townsendii,* USNM, 31326, 31710, 79275, 94253, 169593, 170111, 208105, 203176, 211796–211799, 223964–223967, 225585–225587, 264244.

The measurements were taken as follows (numbers in parentheses refer to Fig. 1): length of cranium, from anterior surface of I^1 to inyon (1–8); length of cranium, from anterior surface of

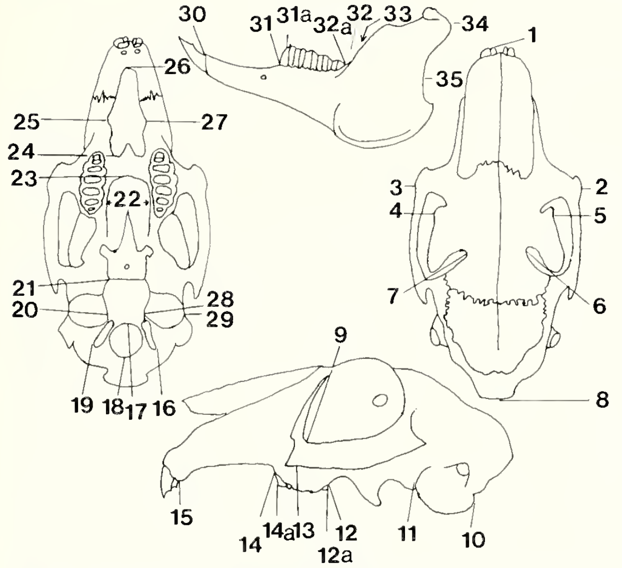

Fig. 1.—Diagram of a leporid skull. The numbers mark the points from which measurements were made and which are referred to in Materials and Methods.

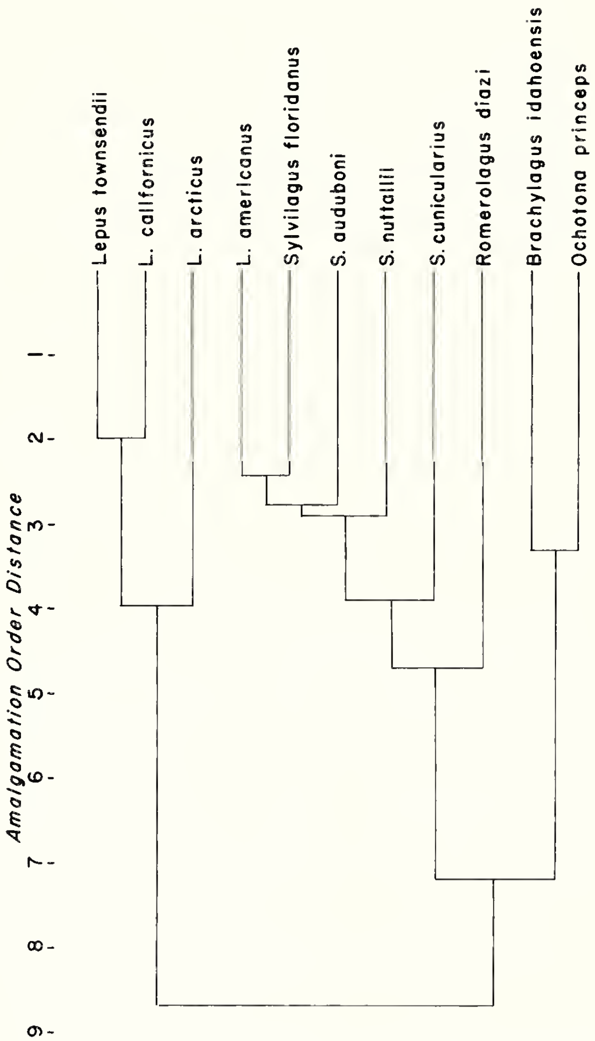

Fig. 2.—Phenogram with amalgamation order distance (Gower, 1967) demonstrating three species groups; 341 means were used in this analysis.

I^1 to ventral margin of foramen magnum (1–17); rostral length, from anterior surface of I^1 to anterior edge of palatal bridge (1–24); length of palatine foramen (24–26); width of palatine foramen (25–27); least AP length of palatal bridge (23–24); posterior edge of palatal bridge to posterior end of basisphenoid (21–23); width of choana posterior to palatal bridge (22); length of basioccipital (17–21); AP diameter tympanic bulla (10–11); width of tympanic bulla (28–29); distance between bullae (20–28); dorsal surface of supraoccipital to dorsal margin of foramen magnum (8–18); width across occipital condyles (16–19); least postorbital constriction (6–7); depth of anterior portion of zygomatic arch (9–13); zygomatic breadth (2–3); width across supraorbital ridges (least interorbital constriction in *Ochotona*) (4–5); length of diastema I^2–P^2 (14–15); length of maxillary tooth row at wear surface (12a–14a); length of maxillary tooth row at alveoli (12–14); AP length I^1; width I^1; width I^2; AP length P_3; width P_3; length of diastema I_1–P_3 (30–31); mandibular foramen to condyloid process (33–34); mandibular foramen to posterior notch of mandible (33–35); length of mandibular tooth row at wear surface (31a–32a); length of mandibular tooth row at alveoli (31–32).

A cluster analysis (Fig. 2) was done with mean values derived from each of 31 variables measured in each of the 11 species mentioned above. Sample size for development of mean values differed between characters but the standard deviations were not significantly large except for length of cranium (1–8, Fig. 1) in *Brachylagus idahoensis* (maximum = 3.7), and we therefore considered the data poolable within a species. Biomedical Computer Program BMDP—2M (University of California, Los Angeles) was employed to compute amalgamation order distance from a sum of squares procedure to produce fusions (see Gower, 1967).

In order to compare the dimensions of our sample measurements of eight species of lagomorphs, we have employed a ratio diagram (Simpson et al., 1960) for 10 mean dimensions which appear to show limited variation within adults of each species (Fig. 3). Although the proportions of the skulls of *Sylvilagus auduboni* and *S. nuttallii* are cottontail-like, and the proportions are jack rabbit-like in *Lepus townsendii*, these were excluded from the diagram to prevent a jumble of lines. Measurements of juvenile specimens were excluded in order to limit occurrence of extreme values affecting our means. *Lepus americanus* was chosen as the standard of comparison. The logs of means were assumed to be zero, while the differences between logs of the mean of the standard and comparable means of species being compared were plotted on the positive (+) or negative (−) sides of the line at zero. The lines presented arbitrarily connect the dots and represent measurements of each taxon represented. Sexual dimorphism proved to be slight; therefore, males and females were combined in all samples analyzed.

Mastication Comparisons

Ardran et al. (1958) made radiograph motion pictures of mastication in *Oryctolagus cuniculus* (L.).

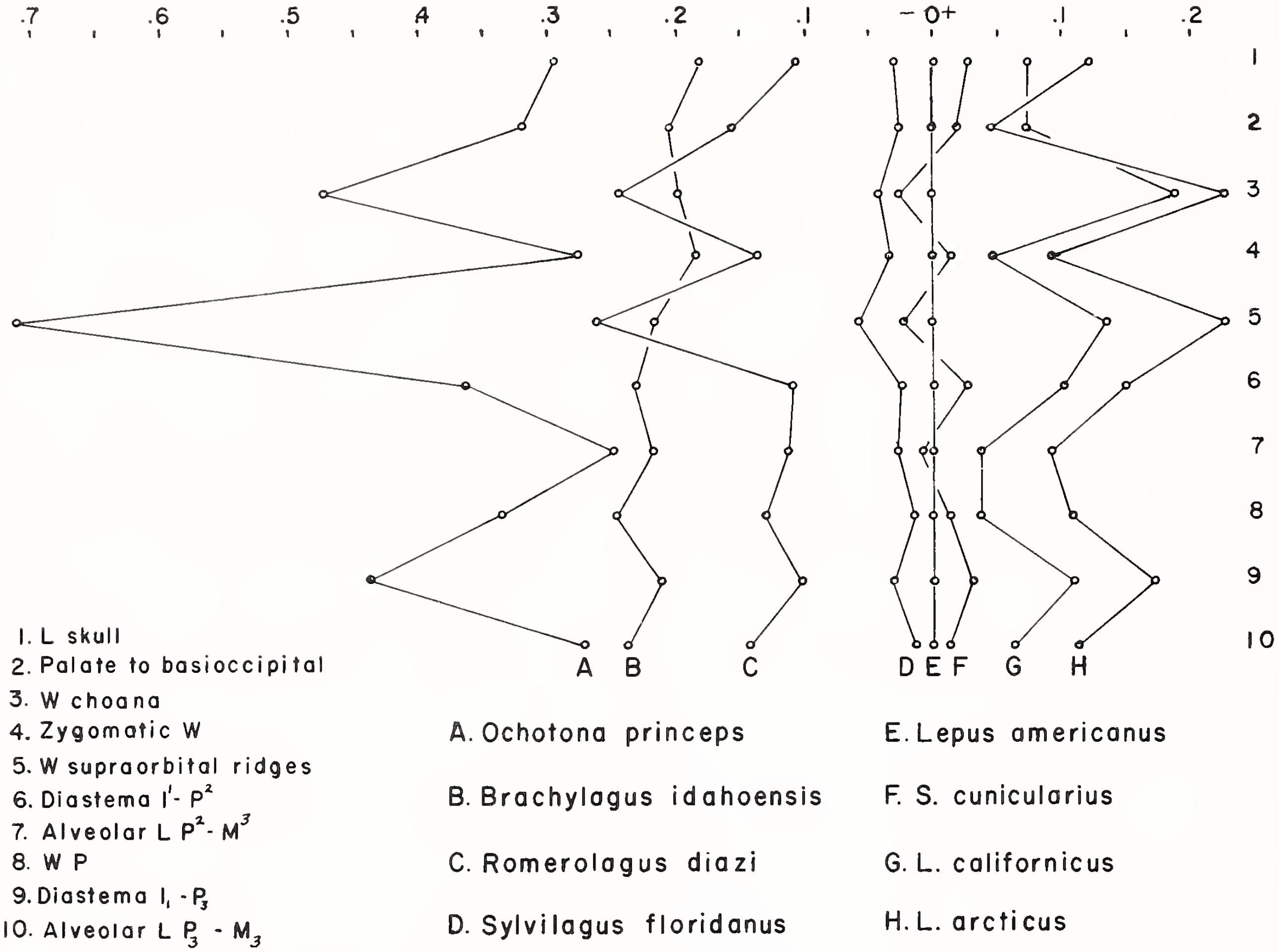

Fig. 3.—Ratio diagram (Simpson et al., 1960) involving the means of 10 characters for 8 species.

We have determined that the same masticatory actions can be inferred by the study of scratches on the enamel of the cheek teeth of living and extinct lagomorphs. The scratches on the ridges of the trigonid portions of the lower and on the anterolophs of the upper cheek teeth are oriented anteroposteriorly, whereas on the talonids and on the posterolophs the scratches are oriented lateromedially. Since the upper tooth rows are markedly farther apart than the lowers, chewing occurs on one side at a time (Ardran et al., 1958:264). When the upper and lower cheek teeth are brought together simultaneously, they provide a series of four cutting edges. In this cutting action the lower cheek teeth slide anteriomediad and the high ridges go down into the depressions between them. The mandible then moves mediad, thus completing a chewing stroke. Since the pattern appears fixed, scratches on the enamel of cheek teeth were examined in the following taxa: *Ochotona princeps, Brachylagus idahoensis, Sylvilagus auduboni, S. cunicularius, S. floridanus, S. nuttallii, Lepus americanus, L. arcticus, L. californicus, L. townsendii, Poelagus majorita, Pentalagus furnessi, Romerolagus diazi, Hypolagus furlongi, H. limnetus, H. regalis, H. vetus, Pratilepus vagus, Paleolagus haydeni,* and *P. hypsodus.*

RESULTS AND DISCUSSION

Analyses of the measurements obtained in this study indicate that the proportions of the skull in *Lepus americanus* are more similar to those in *Sylvilagus auduboni, S. cunicularius, S. floridanus,* and

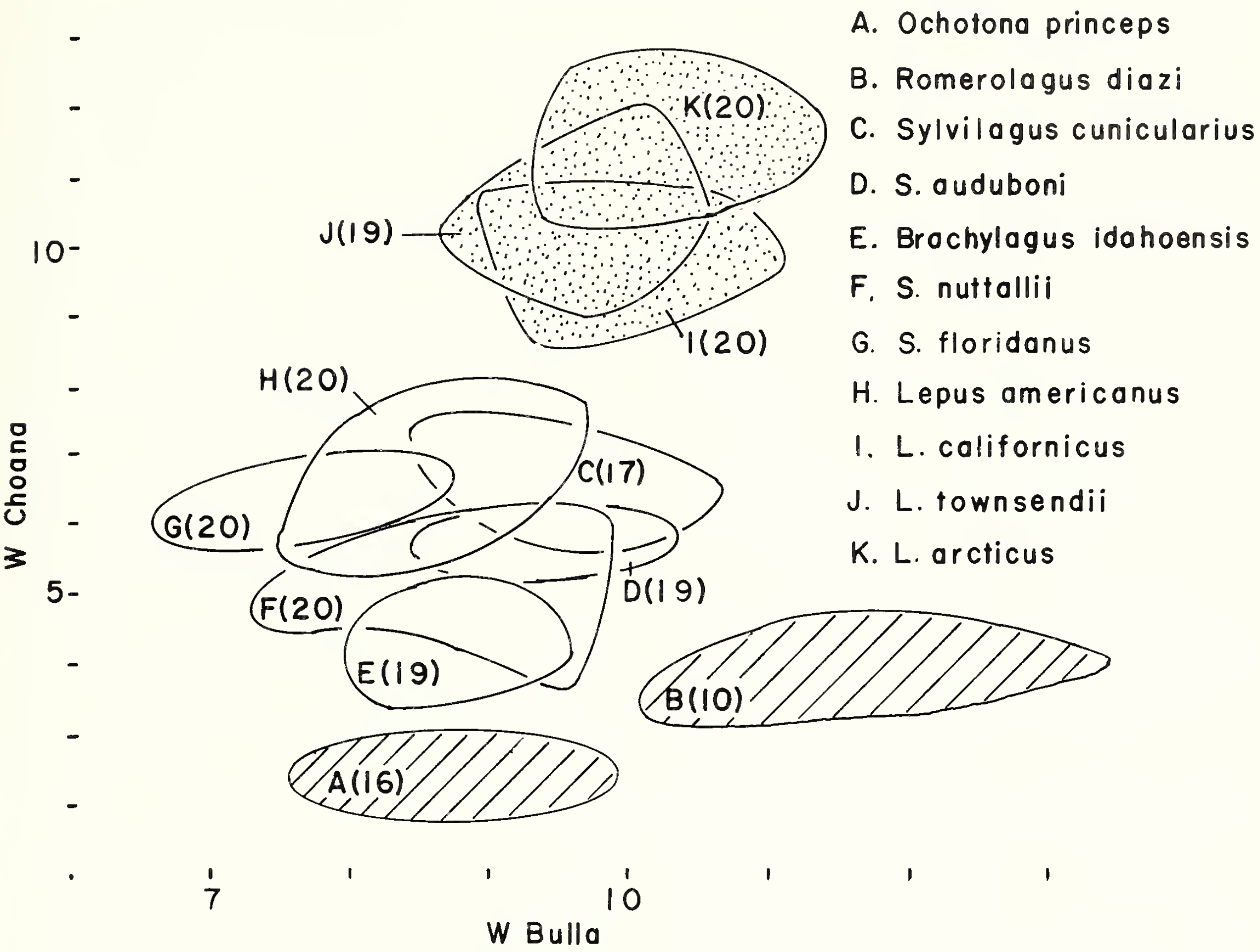

Fig. 4.—Scatter diagram in which the area occupied by each series of dots representing each species is circumscribed. Three ecomorphs are identified by stippling (jack rabbit), unmarked (cottontail), and cross-hatching (rock rabbits). Numbers in parentheses indicate the number of items in each sample. Scale in mm.

S. nuttallii than they are to *L. arcticus, L. californicus,* and *L. townsendii* (Figs. 2–3). It seems significant that the habitat occupied by *L. americanus* is similar to that occupied by *Sylvilagus.* Both are adapted to life in or near forests.

According to Burt (1946:243): "Snowshoe hares [*Lepus americanus*] prefer dense cover during the day, but come out into open areas to feed at night. . . . Customarily, they sit in forms, or on the ground by an old log, or beneath a tree during the daytime. On occasion they seek refuge in hollow logs or burrows in the ground. When startled from a resting spot they usually bound off a short distance and stop. If pursued they almost invariably describe a circle and return to within a few yards of the starting place. . . . Usually, the hare remains within a ten-acre area, and it is difficult to drive one out. This probably is about the size of the home range. Although definite runways are followed, especially in snow, the hares range in all directions when feeding."

On *Sylvilagus floridanus mearnsi,* Burt (1946:248) wrote: "The cottontail is chiefly nocturnal in habits. The day is spent in some sheltered spot, either in a form in heavy grass, a hole in the ground, or the shelter of a brush pile. . . . The home range of an individual averages about three acres for a female and eight acres for a male. Some animals, of course, range much more widely, and others are more restricted in their movements."

Writing on *Sylvilagus nuttallii,* Orr (1940:106) stated: "Upon being disturbed, especially when feeding in tracts of sagebrush, members of this species usually make a short run, anywhere from five to fifteen yards, away from the point of danger. Following this the aroused individual will pause, either facing directly away from or at an angle to the source of disturbance. The ears are held erect and motionless and generally the animal is fairly well screened from observation by the intervening brush. If any further noise or movement is detected by the frightened rabbit it will immediately hop away, following a semi-circular route so as to fool the pursuer and draw attention away from the actual direction of retreat."

Regarding *Lepus europaeus,* Burt (1946:246) stated: "It does not burrow, nor does it customarily seek refuge in an underground passage. Instead, it depends on its keen senses and speed to escape its enemies in the open."

With respect to *Lepus californicus,* Orr (1940:80) wrote: "We may say in general that only open or semiopen country is occupied. The extreme open type is chosen only where there is enough vegetation, even though exceedingly meager, to provide suitable shelter during the daily resting period. Dense areas of chaparral or forested regions, on the other hand, are entirely unsuitable for habitation. Jack rabbits, since they depend for protection upon their ability to run, require open or semiopen land where speed can be attained quickly and enemies can be detected at a considerable distance."

To summarize, in habits and manner of escaping enemies, *Lepus americanus* resembles *Sylvilagus floridanus* and *S. nuttallii,* and not *L. europaeus* and *L. californicus.* Thus in mode of living, *L. americanus* is a functional cottontail and not a jack rabbit, and this relationship correlates, as noted above, with proportions of the skull.

Cluster analysis seems to support the contention that *L. americanus* is more closely related to members of the genus *Sylvilagus* than to other *Lepus* (Fig. 4). However, *Brachylagus idahoensis* is shown to be nearer *Ochotona princeps* than to the other lagomorphs used in this analysis, whereas ratio diagrams (Fig. 2) suggest this species to be nearer in skull proportions to *Lepus americanus, Sylvilagus cunicularius,* and *S. floridanus.* The apparent contradiction can be resolved by examining the habits of *B. idahoensis.* Orr (1940:197), commenting on the manner in which this species escapes its enemies, wrote, "Most rabbits [*B. idahoensis*] are rather wary about running directly into their burrows when closely followed. Pigmy rabbits have been observed to run out of their burrow entrances rather than enter when suddenly frightened. This appears to be a protective type of behavior resorted to in order that inquiry or pursuit may be directed away from their homes." Grinnell et al. (1930) synonymized *Brachylagus* into *Sylvilagus* primarily on ecological grounds. In view of more recent evidence, this assignment is questionable, since *Brachylagus* is distinct from *Sylvilagus* in enamel patterns of P^2 and P_3 (Hibbard, 1963), and in the electrophoretic patterns of hemoglobin (Johnson, 1968). Although this species is known to burrow, and the cluster analysis of skull proportions seem to indicate close relationship to *Ochotona princeps* (Fig. 4), its habits are essentially as in other cottontails, and this, in turn, correlates with other analyses of skull proportions (Figs. 2–3).

Romerolagus diazi is clearly a leporid as indicated by fenestrations on the sides of the rostrum, enamel patterns of the cheek teeth, presence of supraorbital ridges, and presence of M^3. Cluster analysis places *R. diazi* closer to *Sylvilagus* than to *Ochotona,* as one would expect, however, analysis by ratio diagram indicate skull proportions to be near *Ochotona princeps* and not *Sylvilagus.* The width of the choana posterior to palatal bridge and the width across the supraorbital ridges are relatively as in *Ochotona* and unlike other lagomorphs. These characters seem to correlate with what is known of the living habits of *R. diazi,* which are similar to the habits in *Ochotona.* Davis (1944:401) on discussing the habits of *Romerolagus,* wrote: "These small tailless rabbits usually inhabit the dense stands of sacaton grass in the open meadows, but they also frequent crevices in rocky hillsides. They spend much time in underground burrows, which seemingly they dig for themselves, and when above ground, largely early in the morning and late in the afternoon, they resort to runways in the grass." In the genus *Ochotona* there is a variety of habitats, from talus slopes in *O. princeps* of North America to *O. pusilla* in the steppes of Eurasia (Formozov, 1966:214). Walker (1964:648–649), writing on the habits of *Ochotona,* stated: "Species which occur in talus areas live among the rocks. Those which occur in the plains or desert areas dig burrows." *Romerolagus diazi* is known to vocalize, producing a call similar to that in *O. princeps* (Walker, 1964:654). It seems, then, that *R. diazi* lives in a manner similar to rock rabbits, and thus we would propose separating lagomorphs into three groupings (Fig. 5).

The relative width of the choana posterior to the palatal bridge seems to be related to the degree of endurance (Dawson, 1958) or the degree of activity. This seems to be substantiated by noting that jack rabbits, such as *Lepus arcticus, L. californicus,* and *L. townsendii,* have wide choanae; cottontails, such as *Sylvilagus, Brachylagus,* and *L. americanus,* have choanae of intermediate size; and rock rabbits, such as *Romerolagus diazi* and *Ochotona princeps* have the narrowest choanae of all. The length of hind foot is related, in most cases, to running ability and endurance. Jack rabbits are swift runners, cottontails are intermediate in running ability, and rock rabbits are the poorest runners of all. The hind foot in *L. americanus* is relatively longer than in most cottontails, reflecting the "snow shoe" adaptation. Thus, the longer the foot, the wider the choana. In this context it is constructive to point out that the choana in *Felis concolor,* the cougar, is two thirds as wide as that in *Acinonyx trumani,* a cheetah (Adams, 1979; Orr, 1969:2).

The width across the supraorbital ridges (least interorbital constriction in *Ochotona*) is related to the projection of the orbit or line of vision. The wider the supraorbital ridges, the more lateral the line of vision. In jack rabbits the line of vision is lateral, in cottontails (including *L. americanus*) it is intermediate, and in rock rabbits (including *R. diazi*) it is dorsoanteriad (Fig. 2).

The postcranial skeleton of lagomorphs needs to be studied in greater detail to determine if the morphological relationships herein shown for the skull also apply to the postcranial skeleton.

The upper and lower diastemae between the incisors and cheek teeth are proportionally longer in jack rabbits than in other lagomorphs. Presumably this is related to food habits, and research on comparative functions of mastication is needed to clarify this relationship. In all lagomorph taxa the scratches on the enamel were found to be essentially the same. Although the scratches on the enamel in *Mytonolagus* and other Late Eocene specimens were not examined, the known anatomy of the cheek teeth and mandibles strongly suggests that mastication in all lagomorphs is uniform. Thus it can be inferred that mastication in the order has remained unchanged since the Late Eocene.

In all cases, when skulls or fragments of skulls in fossil lagomorphs have been examined, they have been compared, character for character, with living species of ochotonids and leporids (Gazin, 1934; Burke, 1934; MaeInnes, 1953; Wood, 1940; Dawson, 1958, 1969; and Hibbard, 1969). Most of the skull morphology which causes lagomorphs to resemble one another seems to be related to the zygomasseteric structures which profoundly affect the morphology of the lagomorph skull, and, in turn, are related to the difference in diversification between the lagomorphs, which diverged into two families, and the rodents, which diverged into perhaps 43 families.

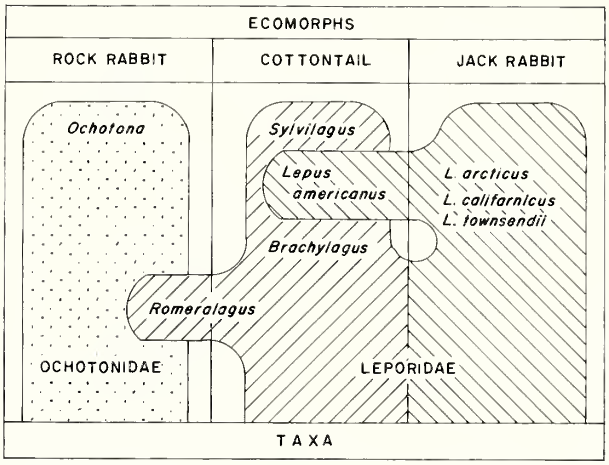

Fig. 5.—Diagram summarizing the distinction between taxa and ecomorphs.

The length of the pinna seems to be related (but not exclusively so) to the degree to which lagomorphs live in or near shelter. Jack rabbits have long ears, cottontails have intermediate ears, and rock rabbits have short ears. *L. arcticus,* a jack rabbit, has relatively short ears, and this seems to be related to the extreme arctic conditions in which it lives.

Clearly phyletic relationships among lagomorphs can not be established from a series of morphological characteristics that are treated equally. To understand the evolutionary history of the order, morphological characters of taxonomic worth should be identified and distinguished from characters which have resulted from convergence. In attempting to differentiate between the two kinds of morphological characters, we propose the term *ecomorph* to *include organisms whose morphological resemblances resulted from convergence owing to ecological preference.*

In North American lagomorphs there are three ecomorphs: **Jack rabbit ecomorph**, which includes *Lepus alleni, L. arcticus, L. callotis, L. californicus, L. flavigularis, L. othus,* and *L. townsendii*; **Cottontail ecomorph**, which includes *Lepus americanus, Brachylagus idahoensis, Sylvilagus aquaticus, S. bachmani, S. braziliensis, S. floridanus, S. insonus, S. nuttallii, S. palustris,* and *S. transitionalis*; and

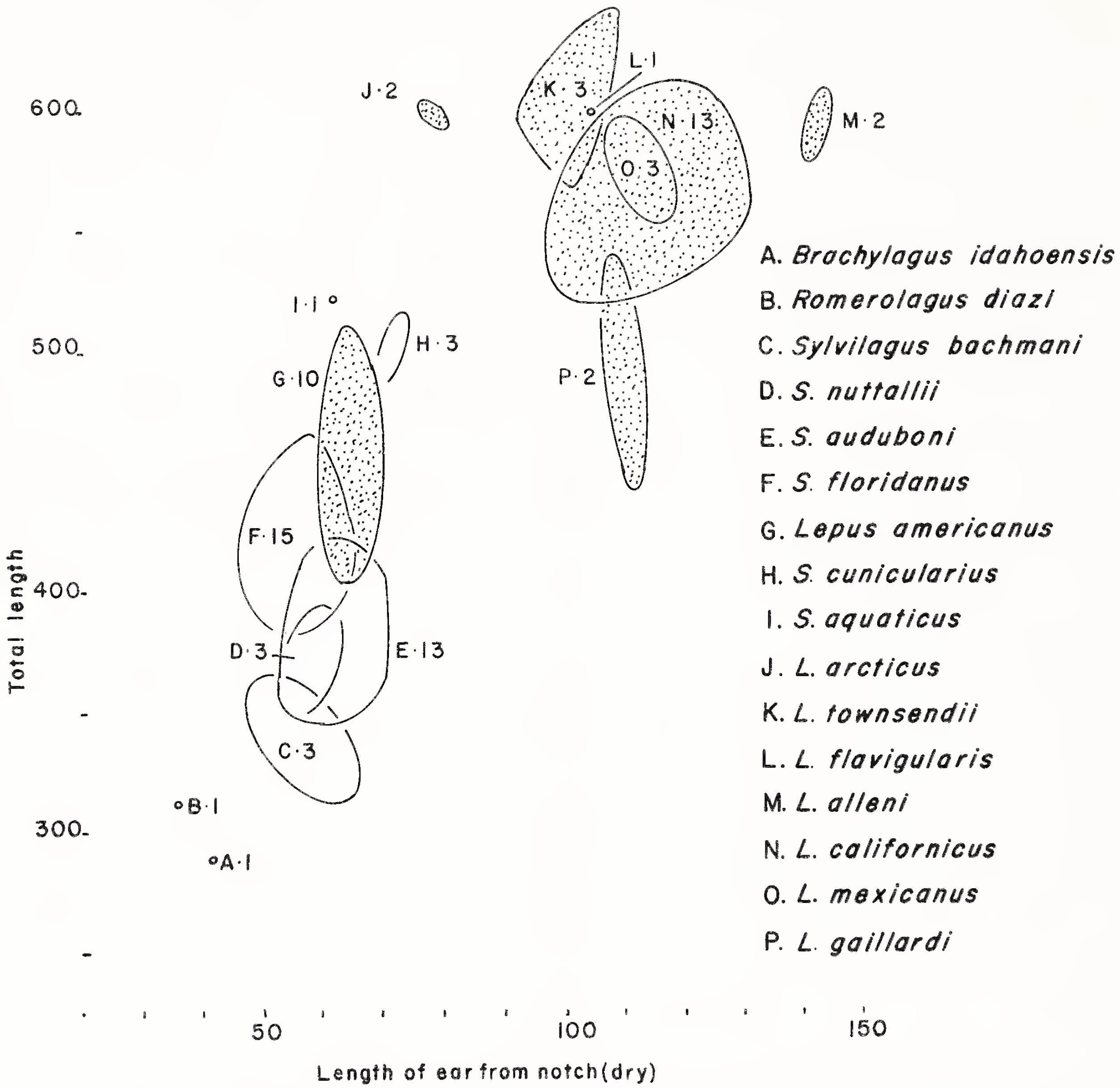

Fig. 6.—Scatter diagram with data from Nelson (1909). Numbers at the right of each letter indicates the number of items in each sample. The area occupied by the series of dots representing each species is circumscribed. Stippling is used to identify the genus *Lepus*. Scale in mm.

Rock rabbit ecomorph, which includes *Romerolagus diazi* and *Ochotona princeps* (Fig. 5). The three ecomorphs are related to three broad habitats: open country such as plains, sagebrush flats, tundra, etc. (jack rabbit ecomorph); forest margins and thickets (cottontail ecomorph); and rock slides and grasslands (rock rabbit ecomorph).

Comparable studies on such groups as sciurids and erethyzontids are almost certain to lead to recognition of ecomorphs. Tree squirrels (*Sciurus, Tamiasciurus,* etc.), for example, have a wide interorbital breadth whereas in ground squirrels (*Spermophilus,* etc.) it is far narrower. This tends to project lines of vision differently in the two kinds of squirrels (White, 1970:12), thus suggesting tree squirrel and ground squirrel ecomorphs.

It seems, therefore, that some osteological characters imply a common ancestry whereas others correlate with habits and are the result of convergence. A distinction needs to be made between a taxon and an ecomorph. This distinction is seldom clear, since it involves dealing with the interaction between selective forces and phenotypes (ultimately genotypes) through a spectrum of structural and functional variations, and only characters which are near each end of the spectrum can provide distinctions. Thus in lagomorphs, characters resulting presumably from similar selective pressures are identified by their functions or presumed functions with respect to habits and other ecological factors. Some such characters are: 1) width of choana; 2) degree of development of supraorbital ridges; 3) posture, as implied by the flexion of the basicranial basifacial axis; 4) relative length of hind foot; and 5) length of upper and lower diastemae between incisors and cheek teeth.

At the other end of the above spectrum, characters which are presumed to be "independent" of any apparent selective forces, and on which most systematic decisions are based, are as follows in lagomorphs: 1) enamel tooth patterns; 2) hypsodonty and degree of rooting of cheek teeth; and 3) altricial versus precocial young.

In summary, we have shown that when a lagomorph hierarchy is intercepted, three clusters appear (Fig. 5). *Ochotona princeps* and *Brachylagus idahoensis* appear as a distinct group from the *Sylvilagus* grouping (including *Lepus americanus* and *Romerolagus diazi*) and the remaining species of *Lepus*. Such an analysis fails to separate the groupings of hares, rabbits, and pikas (taxa), or the groupings of jack rabbits, cottontails, and rock rabbits (ecomorphs), because we know of no method to separate characters which were convergently developed from those inherited from a common ancestor. Cluster analysis thus confirms our contention that taxonomic similarities cannot be obtained from characteristics randomly selected and analyzed by methods of numerical taxonomy.

As a check on our analyses we obtained "external" data from Nelson (1909) and plotted the total length against length of ear from notch (dry). The results (Fig. 6) show agreement with our analysis of, especially, *Lepus americanus*.

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LITERATURE CITED

Adams, D. B. 1979. The cheetah: native American. Science, 205(4411):1155–1158.

Ardran, G. M., F. H. Kemp, and W. D. L. Ride. 1958. A radiographic analysis of mastication and swallowing in the domestic rabbit: *Oryctolagus cuniculus* (L.). Proc. Zool. Soc. London, 130(2):257–274.

Burke, J. J. 1934. *Mytonolagus*, a new leporine genus from the Uinta Eocene series in Utah. Ann. Carnegie Mus., 23:399–420.

Burt, W. H. 1946. The mammals of Michigan. Univ. Michigan Press, Ann Arbor, 288 pp.

Craigie, E. H. 1948. Bensley's practical anatomy of the rabbit. Univ. Toronto Press, Toronto, 391 pp.

Davis, W. B. 1944. Notes on Mexican mammals. J. Mamm., 25:370–403.

Dawson, M. R. 1958. Later Tertiary Leporidae of North America. Univ. Kansas Paleont. Contrib., Vertebrata, 6:1–75.

———. 1969. Osteology of *Prolagus sardus*, a Quaternary ochotonid (Mammalia, Lagomorpha). Palaeovertebrata, 2:157–191.

Formozov, A. N. 1966. Adaptive modification of behavior in mammals of the Eurasian Steppes. J. Mamm., 47:208–223.

Gazin, C. L. 1934. Fossil hares from the Late Pliocene of southern Idaho. Proc. U.S. Nat. Mus., 83(2976):111–121.

Gower, J. C. 1967. A comparison of some methods of cluster analysis. Biometrics, 23:623–637.

Grinnell, J., J. Dixon, and J. M. Linsdale. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. Univ. California Publ. Zool., 35:1–594.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. Ronald Press, New York, 546 pp.

Hibbard, C. W. 1963. The origin of the P_3 pattern of *Sylvilagus, Caprolagus, Oryctolagus,* and *Lepus*. J. Mamm., 44:1–15.

———. 1969. The rabbits (*Hypolagus* and *Pratilepus*) from the upper Pliocene, Hagerman local fauna of Idaho. Michigan Academician, Papers Michigan Acad. Sci., Arts, and Letters, 1(1):81–97.

Johnson, M. L. 1968. Application of blood protein electrophoretic studies to problems in mammalian taxonomy. Syst. Zool., 17:23–30.

MacInnes, D. G. 1953. The Miocene and Pleistocene Lagomorpha of East Africa. British Mus. (Nat. Hist.), Fossil Mamm. Africa, 6:1–30.

Nelson, E. W. 1909. The rabbits of North America. North Amer. Fauna no. 29:1–314.

Orr, P. C. 1969. *Felis trumani* a new radiocarbon dated cat skull from Crypt Cave, Nevada. Bull. Santa Barbara Mus. Nat. Hist., Dept. Geol., 2:1–8.

Orr, R. T. 1940. The rabbits of California. Occas. Papers California Acad. Sci. 19:1–227.

Simpson, G. G., A. Roe, and R. C. Lewontin. 1960. Quantitative Zoology (rev. ed.). Harcourt, Brace and Co., New York, 440 pp.

Walker, E. P. 1964. Mammals of the World. Johns Hopkins Press, Baltimore, 1,500 pp.

White, J. A. 1970. Late Cenozoic porcupines (Mammalia, Erethyzontidae) of North America. Amer. Mus. Novit., 2421: 1–15.

Wood, A. E. 1940. The mammalian fauna of the White River Oligocene. Pt. III. Lagomorpha. Amer. Phil Soc., Trans., new series, 28:271–362.

———. 1957. What, if anything, is a rabbit? Evolution, 11: 417–425.

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PALEOCENE AND EOCENE RODENTS OF NORTH AMERICA

Craig C. Black and John F. Sutton

ABSTRACT

The record of Paleocene and Eocene rodents from North America is reviewed. Approximately twice as many early Tertiary genera of rodents are recognized now as were at the time of Wilson's earlier review (1949) of this record. Rodent origins are discussed, and a family and higher level classification proposed. A family level review emphasizes the variety within the protrogomorphous rodents and demonstrates several independent developments of the sciuromorphous, myomorphous, and hystricomorphous zygomasseteric complexes. Geographic distribution of several late Eocene and/or early Oligocene myomorphs supports the concept of radiation of these rodents northward from Central American centers.

INTRODUCTION

In 1949 Robert W. Wilson published a most comprehensive and useful review of early Tertiary rodents of North America. His contribution discussed almost all aspects of early rodent differentiation, stratigraphic and faunal occurrence, and classification, together with detailed summaries of the evolution of family and subfamily groups. Somewhat more than a quarter of a century later, it seems appropriate to examine some aspects of the present state of our knowledge of this group and we can think of no better starting point than Wilson's previous summary. We will follow his format but only to update the information contained therein; a great deal of what he presented is as valid today as it was then. His general diagnoses of suborders and families and descriptions of genera known at that time will not be repeated here.

Wilson (1949:86) stated that, as a conservative estimate, more than one-half of all potentially known North American early Tertiary rodents had been described. At that time 19 genera of Eocene rodents were known if one recognizes "*Mysops kalicola*" as distinct from true *Mysops*. Since 1949, 13 new genera have been described from the Eocene, three additional from the earliest Oligocene Porvenir fauna of Texas, and at least four new genera from the Eocene are now being described. Thus, as many new North American early Tertiary genera have been recognized in the last 30 years as had been known from all work previous to 1949. How many more may yet be found is a moot question.

While Wilson considered all North American rodents from the late Paleocene into the early Miocene in his review, with three exceptions we shall restrict our coverage to those occurring in the Paleocene and Eocene. One of the several faunas of the Vieja Group in Trans Pecos Texas poses a particular problem. The Porvenir local fauna (J. A. Wilson, 1978; Wood, 1974) is considered to be of earliest Oligocene age. However, J. A. Wilson (1978:37) suggested that it is of the same age as the La Point fauna of Utah, which most workers consider to be Duchesnean, latest Eocene. A number of the Porvenir rodents bear closer resemblance to late Eocene species elsewhere than they do to early Oligocene ones. This may be due to the longer temporal persistence of some lineages in the southern parts of their range, or it may indicate an actually older age for the Porvenir fauna. Whether latest Eocene or earliest Oligocene, the rodents of the Porvenir will be discussed in this paper.

Likewise, two rodent assemblages from Mexico, both quite small, will be considered. Those from the Rancho Gaitan local fauna are again of late Eocene or early Oligocene age, quite similar to those from the Porvenir assemblage. Rodents from near Guanajuato in central Mexico are of unknown age but are of late Eocene or early Oligocene aspect.

STUDIES SINCE 1949

Much new information concerning rodent evolution and occurrence has accumulated since 1949. Of particular significance is the work done by A. E. Wood on Eocene ischyromyids and on the new rodent assemblages from Texas (Wood, 1973, 1974) and the overall review of the Rodentia by Stehlin and Schaub (1951). Faunas with new rodents from the Big Horn Basin (Bown, 1979) and the Wind

River Basin (Guthrie, 1967, 1971) have been described. A major new mid-Eocene suite of rodents has been discovered in Utah (Dawson, 1968) and additional work has been done on the California faunas (Golz and Lillegraven, 1977; Lillegraven, 1977; Lindsay, 1968) and those from the Green River Basin in Wyoming (West, 1973). The general picture, geographically, is shown in Fig. 1.

In addition to the new taxa described since 1949, much new information has been gained on species only poorly known at that time, both through recovery of new material and through reexamination of the older collectings using new techniques. Studies by Wahlert (1974) on the cranial foramina of rodents and on the microstructure of incisor enamel (Wahlert, 1968 and in progress) and work by Guthrie (1963) and Bugge (1974) on the carotid circulation in rodents are useful approaches to solving the problems of rodent relationships.

RODENT ORIGINS

Although there has been a significant increase in our knowledge of rodent differentiation since Wilson's 1949 review, there has been essentially no new information on rodent origins. This is not to say, however, that there has not been considerable speculation and discussion of the topic.

The earliest reported rodent is still *Paramys atavus* from the late Paleocene Eagle Coal Mine, Bear Creek, Montana. Wood (1962) reviewed the material of *P. atavus* and an additional tooth was described by McKenna (1961). Wood (1962:252–254) discussed the various speculations concerning rodent origins and suggested an early to early-middle Paleocene date for their differentiation. He favored a possible common ancestry with the primates. In a discussion of the tarsus of early eutherians, Szalay and Decker (1974:257) advocated a paleoryctid or leptictid ancestry for rodents. McKenna (1975:37) agreed and suggested that rodents may have arisen from a *Cimolestes*-like stock in the latest Cretaceous or earliest Paleocene. In the classification of the Mammalia presented in that paper (McKenna, 1975: 40–41), he leaves the rodents as Cohort Epitheria, *incertae sedis,* not assigning the order to his Grandorder Ferae, to which *Cimolestes* is basal. More recently, some suggestion of rodent affinities has been seen in the Paleocene eurymylid *Heomys* (Li, 1977).

CLASSIFICATION

In the classification presented here we restrict our coverage to those higher taxonomic units represented in the North American record (see Fig. 2). The classification in part follows Wood (1955, 1962), but there are a number of modifications. Within the Suborder Protrogomorpha we recognize two superfamilies. We follow Simpson (1945), Wilson (1949), and Black (1968*a,* 1971) in placing the Paramyidae (Wood, 1962) in the Family Ischyromyidae. The Prosciurinae are transferred from the Ischyromyidae to the Aplodontidae following Rensberger (1975). In light of Wahlert's (1973) work on *Protoptychus,* the Family Protoptychidae is not placed subordinally. This form may well prove to be more closely related to the South American Caviomorpha than to any other group. The Eutypomyidae are removed from the Castorimorpha and the Gliridae from the Myomorpha with both families left without subordinal allocation. As we learn more about early rodent differentiation, it becomes increasingly apparent that the sciuriomorph, myomorph, and hystricomorph zygomasseteric structure evolved independently several times for each condition.

Order Rodentia Bowditch, 1821

Suborder Protrogomorpha Zittel, 1893
  Superfamily Ischyromyoidea Wood, 1937
    Family Ischyromyidae Alston, 1896
    Family Sciuravidae Miller and Gidley, 1918
    Family Cylindrodontidae Miller and Gidley, 1918
  Superfamily Aplodontoidea Matthew, 1910
    Family Aplodontidae Trouessart, 1887
    Family Mylagaulidae Cope, 1881
Uncertain Suborder
    Family Protoptychidae Wood, 1937
Uncertain Suborder
    Family Eutypomyidae Miller and Gidley, 1918

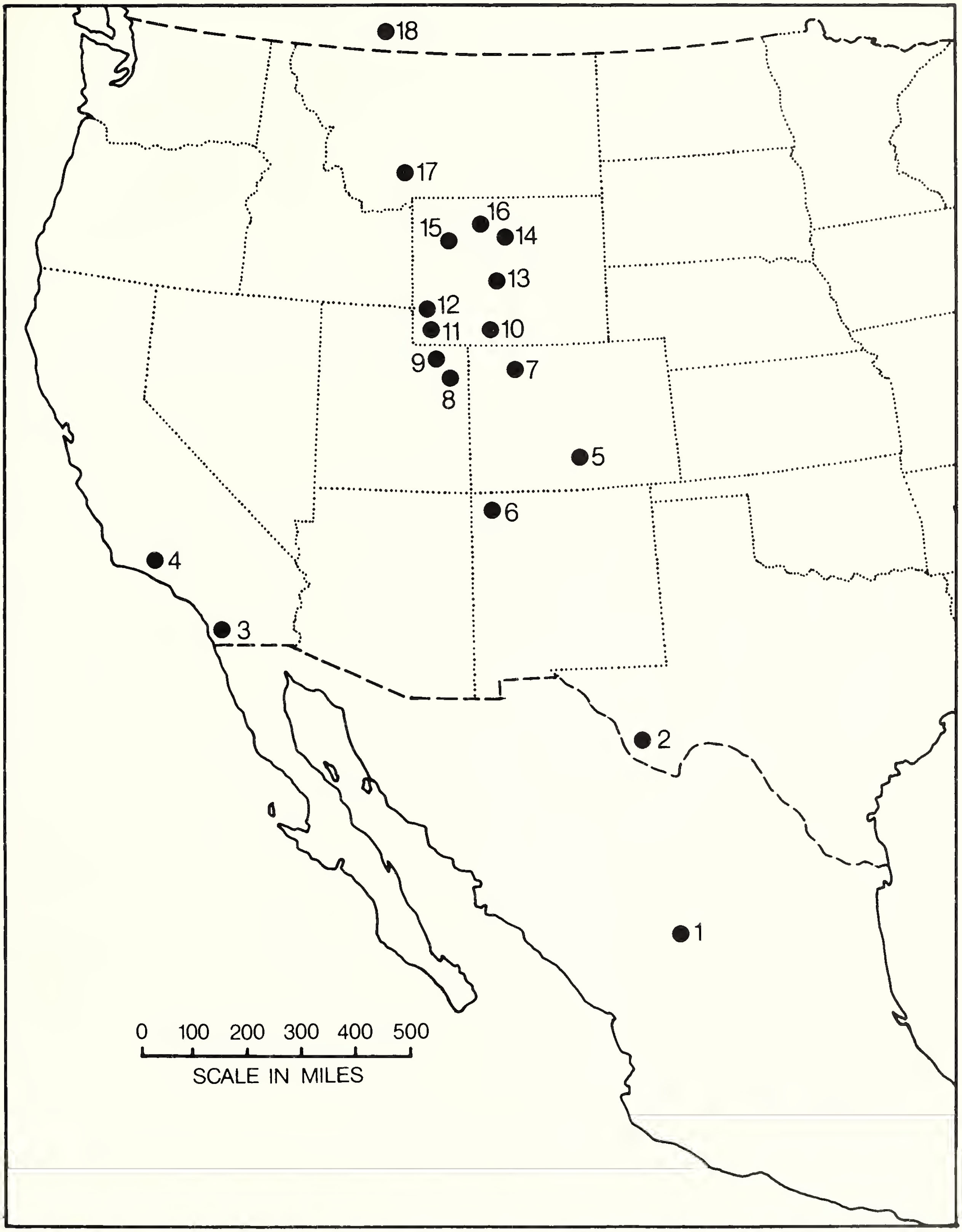

Fig. 1.—Map showing location of principal rodent occurrences. 1, Guanajuato. 2, Vieja Group Texas. 3, Poway Formation. 4, Sespe Formation. 5, San Juan Basin. 6, Huerfano Formation. 7, Sand Wash Basin. 8, Powder Wash Green River Formation. 9, Uinta Basin. 10, Washakie Basin. 11, Bridger Basin. 12, Fowkes Formation. 13, Wind River Formation. 14, Badwater Localities. 15, Big Sandy-New Fork Area. 16, Big Horn Basin. 17, Shoddy Springs. 18, Swift Current Creek.

	BEAR CREEK, MONT.	WILLWOOD	NOWATER	BITTER CREEK	POWDER RIVER	FOUR MILE	W. OF ELK MOUNTAIN	LYSITE	ALMAGRE	WILLWOOD	KNIGHT STATION	FOSSIL BUTTE	LOST CABIN	HUERFANO A (lower)	LARGO	WILLWOOD	LA BARGE	DAD	NEW FORK	CATHEDRAL BLUFF (GAZIN)	HUERFANO B (upper)
ISCHYROMYIDAE																					
Paramys atavus	●				●																
Paramys excavatus		●	●	●			●	●		●	●		●	●			●		●	●	●
Paramys copei		●			●	●		●	●				●		●		●	●		●	●
Lophiparamys murinus		●											●								
Franimys buccatus		●						●	●	●			●		●						
Paramys francesi			●										●								
Franimys amherstensis			●																		
Leptotomus loomsi								●													
Pseudotomus coloradensis								●					●								
Franimys lysitensis								●													
Lophiparamys debequensis								●					●								
Lophiparamys woodi													●								
Thisbemys perditus													●								
Reithroparamys pattersoni													●								
Leptotomus grandis														●							
Leptotomus costilloi														●							
Paramys huerfanensis																				●	●
Reithroparamys huerfanensis																				●	●
Reithroparamys delicatissimus																				●	
Thisbemys nini																					●
Leptotomus huerfanensis																					●
Reitaroparamys matthewi																					
Paramys wyomingensis																					
Paramys delicatior																					
Microparamys minutus																					
Paramys delicatus																					
Pseudotomus robustus																					
Pseudotomus hians																					
Ischyrotomus superbus																					
Ischyrotomus horribilis																					
Microparamys wilsoni																					
Thisbemys plicatus																					
Leptotomus parvus																					
Microparamys wyomingensis																					
Ischyrotomus oweni																					

Fig. 2.—Distribution of early Tertiary species of rodents in North America. Species are listed by family in approximate order of stratigraphic occurrence. *Microparamys lysitensis* from the Lysite fauna was inadvertently omitted. Only named species are listed with literature references to *Paramys* sp., *Microparamys* sp., etc. not included.

GREEN LOCALITY (CATHEDRAL BLUFF)	BLACK'S FORK	TWIN BUTTES	BRIDGER LEVEL (see Wilson, 1949)	GREEN RIVER, UINTA BEDS	WHISTLER'S SQUAT	BRIDGER, BIG SANDY	POWDER WASH	THOMAS CANYON	SAND WASH	WAGONHOUND	WASHAKIE B	POWAY	MYTON	RANDLETT	SWIFT CURRENT CREEK	SAN DIEGO	VENTURA (SESPE)	HENDRY RANCH	HARTMAN RANCH	TAPO RANCH	HENDRY RANCH (Locality 20)	CANDELARIA	RANCHO GAITAN	LA POINT	PEARSON RANCH	PORVENIR	GUANAJUATO
●						●		●																			
●																											
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(CONTINUED)

	BEAR CREEK, MONT.	WILLWOOD	NOWATER	BITTER CREEK	POWDER RIVER	FOUR MILE	W. OF ELK MOUNTAIN	LYSITE	ALMAGRE	WILLWOOD	KNIGHT STATION	FOSSIL BUTTE	LOST CABIN	HUERFANO A (lower)	LARGO	WILLWOOD	LA BARGE	DAD	NEW FORK	CATHEDRAL BLUFF (GAZIN)	HUERFANO B (upper)
Thisbemys corrugatus																					
Leptotomus bridgerensis																					
Thisbemys uintensis																					
Ischyrotomus petersoni																					
Leptotomus grangeri																					
Leptotomus leptos																					
Reithroparamys californicus																					
Ischyrotomus californicus																					
Ischyrotomus littoralis																					
Leptotomus caryophilus																					
Ischyrotomus eugenei																					
Reithroparamys gidleyi																					
Leptotomus sciuroides																					
Leptotomus mytonensis																					
Thisbemys medius																					
Mytonomys robustus																					
Ischyrotomus compressidens																					
Leptotomus kayi																					
Mytonomys burkei																					
Microparamys tricus																					
Leptotomus tapensis																					
Rapamys fricki																					
Leptotomus guildayi																					
Microparamys dubius																					
Manitsha johanniculi																					
Mytonomys gaitania																					
Eohaplomys tradux																					
Eohaplomys matutinus																					
Eohaplomys serus																					
Leptotomus gigans																					
Microparamys perfossus																					
Ischyrotomus cf. petersoni																					
Manitsha johanniculi																					
Ischyromys blacki																					
Guanajuatomys hibbardi																					

GREEN LOCALITY (CATHEDRAL BLUFF)	BLACK'S FORK	TWIN BUTTES	BRIDGER LEVEL (see Wilson, 1949)	GREEN RIVER, UINTA BEDS	WHISTLER'S SQUAT	BRIDGER, BIG SANDY	POWDER WASH	THOMAS CANYON	SAND WASH	WAGONHOUND	WASHAKIE B	POWAY	MYTON	RANDLETT	SWIFT CURRENT CREEK	SAN DIEGO	VENTURA (SESPE)	HENDRY RANCH	HARTMAN RANCH	TAPO RANCH	HENDRY RANCH (Locality 20)	CANDELARIA	RANCHO GAITAN	LA POINT	PEARSON RANCH	PORVENIR	GUANAJUATO
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	BEAR CREEK, MONT.	WILLWOOD	NOWATER	BITTER CREEK	POWDER RIVER	FOUR MILE	W. OF ELK MOUNTAIN	LYSITE	ALMAGRE	WILLWOOD	KNIGHT STATION	FOSSIL BUTTE	LOST CABIN	HUERFANO A (lower)	LARGO	WILLWOOD	LA BARGE	DAD	NEW FORK	CATHEDRAL BLUFF (GAZIN)	HUERFANO B (upper)
SCIURAVIDAE																					
Knightomys depressus								●					●								
Knightomys senior																	●			●	
Sciuravus wilsoni																			●	●	
Pauromys schaubi																					
Sciuravus bridgeri																					
Sciuravus nitidus																					
Tillomys parvidens																					
Taxymys lucaris																					
Tillomys senex																					
Pauromys perditus																					
Sciuravus rarus																					
Taxymys progressus																					
Sciuravus eucristadens																					
Sciuravus altidens																					
Sciuravus popi																					
Sciuravus powayensis																					
CYLINDRODONTIDAE																					
Dawsonomys minor								●					●								
Dawsonomys woodi																	●				
Mysops fraternus																					
Mysops minimus																					
Mysops parvus																					
Mysops boskeyi																					
Pareumys troxelli																					
Paureumys grangeri																					
Pareumys milleri																					
Presbymys lophatus																					
Pseudocylindrodon tobeyi																					
Pareumys guensburgi																					
Jaywilsonomys ojinagaensis																					
Jaywilsonomys pintoensis																					
Pseudocylindrodon neglectus																					

GREEN LOCALITY (CATHEDRAL BLUFF)	BLACK'S FORK	TWIN BUTTES	BRIDGER LEVEL (see Wilson, 1949)	GREEN RIVER, UINTA BEDS	WHISTLER'S SQUAT	BRIDGER, BIG SANDY	POWDER WASH	THOMAS CANYON	SAND WASH	WAGONHOUND	WASHAKIE B	POWAY	MYTON	RANDLETT	SWIFT CURRENT CREEK	SAN DIEGO	VENTURA (SESPE)	HENDRY RANCH	HARTMAN RANCH	TAPO RANCH	HENDRY RANCH (Locality 20)	CANDELARIA	RANCHO GAITAN	LA POINT	PEARSON RANCH	PORVENIR	GUANAJUATO
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	BEAR CREEK, MONT.	WILLWOOD	NOWATER	BITTER CREEK	POWDER RIVER	FOUR MILE	W. OF ELK MOUNTAIN	LYSITE	ALMAGRE	WILLWOOD	KNIGHT STATION	FOSSIL BUTTE	LOST CABIN	HUERFANO A (lower)	LARGO	WILLWOOD	LA BARGE	DAD	NEW FORK	CATHEDRAL BLUFF (GAZIN)	HUERFANO B (upper)
Pseudocylindrodon tekanus																					
Ardynomys occidentalis																					
APLODONTIDAE																					
Spurimus selbyi																					
Spurimus scotti																					
EUTYPOMYIDAE																					
"Mysops" kalicola													●								
Janimus rhinophilus																					
Eutypomys inexpectatus																					
PROTOPTYCHIDAE																					
Protoptychus hatcheri																					
Protoptychus smithi																					
EOMYIDAE																					
"Namatomys" fantasma																					
Protoadjidaumo typus																					
Adjidaumo minutus																					
Viejadjidaumo magmscopuli																					
Aulolithomys bounities																					
Yoderimys lustrorum																					
INCERTAE SEDIS																					
Simimys simplex																					
Simimys vetus																					
Simimys murinus																					
Prolapsus sibilatoris																					
Prolapsus junctionis																					
Griphomys toltecus																					
Griphomys alcer																					
Floresomys guanajuatoensis																					

GREEN LOCALITY (CATHEDRAL BLUFF)	BLACK'S FORK	TWIN BUTTES	BRIDGER LEVEL (see Wilson, 1949)	GREEN RIVER, UINTA BEDS	WHISTLER'S SQUAT	BRIDGER, BIG SANDY	POWDER WASH	THOMAS CANYON	SAND WASH	WAGONHOUND	WASHAKIE B	POWAY	MYTON	RANDLETT	SWIFT CURRENT CREEK	SAN DIEGO	VENTURA (SESPE)	HENDRY RANCH	HARTMAN RANCH	TAPO RANCH	HENDRY RANCH (Locality 20)	CANDELARIA	RANCHO GAITAN	LA POINT	PEARSON RANCH	PORVENIR	GUANAJUATO
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Suborder Sciuromorpha Brandt, 1855
  Superfamily Sciuroidea Gill, 1872
    Family Sciuridae Gray, 1821
Suborder Castorimorpha Wood, 1955
  Superfamily Castoroidea Gill, 1872
    Family Castoridae Gray, 1821
Suborder Myomorpha Brandt, 1855
  Superfamily Muroidea Miller and Gidley, 1918
    Family Cricetidae Rochebrune, 1883
    Family Muridae Gray, 1883
    Family Arvicolidae Gray, 1821
  Superfamily Dipodoidea Weber, 1904
    Family Zapodidae Coues, 1875
    Family Dipodidae Waterhouse, 1842
  Superfamily Geomyoidea Weber, 1904
    Family Eomyidae Deperet and Douxami, 1902
    Family Heteromyidae Allen and Chapman, 1893
    Family Geomyidae Gill, 1872

Suborder Protrogomorpha

This suborder is now most frequently used to unite those rodent families in which there has been no specialization of the masseter muscle complex and hence modification of the zygoma, snout, and infraorbital foramen. The origin of the masseter is limited to the ventral surface of the zygoma in all cases but one, and the infraorbital foramen is moderately large and circular. The dental formula is 1/1, 0/0, 2/1, 3/3 except in mylagaulids where P3, and, in some forms, M3/3 are lost.

It is quite probable, as A. E. Wood has stated in numerous publications (see particularly 1962), that all other rodents evolved from this group. It also is becoming clear that the myomorphous, sciuromorphous, and hystricomorphous conditions each arose more than once from the protrogomorphous condition. Two superfamilies make up the Suborder, the Ischyromyoidea and the Aplodontoidea.

Family Ischyromyidae

A great deal has been written about members of this family since 1949 with work done by Wood (1962, 1974, and 1976) being of paramount importance. The classification followed here recognizes a single family in contrast to Wood, who recognizes two families, the Paramyidae and the Ischyromyidae, for the rodents here considered to belong in the Ischyromyidae. Regardless of the level of taxonomic separation, we believe there is agreement that these rodents are more closely related to one another than they are to any other rodent family.

Wood (1976, Table 2) separates *Ischyromys* and *Titanotheriomys* from all other ischyromyids on the basis of zygomasseteric structure and supposed changes in a number of cranial foramina. Black (1968*a*, 1971) considered *Titanotheriomys* to be a synonym of *Ischyromys* and included all paramyines within the single Family Ischyromyidae. Wood (1976:374) states, "whether *Titanotheriomys* was sciuromorphous or myomorphous, it clearly had no relationships with other sciuromorphous or myomorphous rodents and seems to have left no descendants." Specimens referred to "*Titanotheriomys*" actually display the entire range of zygomasseteric structure from *protrogomorphous* to "*subsciuromorphous*" with only the extreme subsciuromorphous skulls possibly distinguishable from *Ischyromys*. This entire series of forms clearly has a close relationship to typical *Ischyromys*, which in turn appears to have evolved from a *Leptotomus*-like paramyine. *Ischyromys* may well be represented in the late Eocene (Black, 1971:203), suggesting a late Bridgerian or early Uintan origin for the genus.

Of the new genera of ischyromyids described since 1949, *Microparamys* (Wood, 1959*b*) is perhaps the most significant. *Microparamys* is known throughout the Eocene and into the early Oligocene in North America and from the early Eocene of Europe. This genus has been discussed by Wood (1962) and by Dawson (1966, 1968, 1974) and both have suggested that *Microparamys* may have shared a common ancestry with the Sciurividae. Hartenberger (1971) thought the European early Eocene *Microparamys* were ancestral to the Gliridae. Dawson (1974:149) suggested that the disappearance of *Microparamys* in North America may have been related to the radiation of eomyids in the early Oligocene.

Other genera of ischyromyids not known prior to 1949 appear to be closely related to, but more specialized than, *Paramys* and *Leptotomus*. These include *Mytonomys* (Wood, 1956; Black, 1968*b*) and *Thisbemys* (Wood, 1959*b*). *Franimys* (Wood, 1962) is close to *Reithroparamys*. New material of *Pseudotomus*, *Ischyrotomus*, and *Manitsha* has shown that these genera are closely related and form a phyletic sequence.

Family Sciuravidae
(By Mary R. Dawson)

Wilson (1949:96–98) pointed out clearly the morphological distinctions of the Sciuravidae (treated by him as the Subfamily Sciuravinae, Family Ischyromyidae) from other Eocene rodents. "Of prime importance" to Wilson was the pattern of the upper molars, which have a well developed hypocone separated from the protocone by a pronounced valley, reduction of conules, and several different types of lophs. The phylogenetic importance of the sciuravids was also emphasized by Wilson (1949:96–98, 122, 152–155), who considered them the best possible ancestral group known at the time for the dipodoids, muroids, and geomyoids.

The family still stands as a distinctive unit. Work since 1949 has added the genera *Knightomys* and *Dawsonomys* (Gazin, 1961, 1962), although the latter may not be a sciuravid; has filled in the fossil record of the family, which ranges from Lysitean to Duchesnean; and has contributed to its known morphological picture (Dawson, 1961, 1962, 1966, 1968; Wood, 1959*a*, 1965). The family is exclusively an Eocene one, unless the early Oligocene genus *Yoderimys*, usually considered an aberrant eomyid, is a sciuravid. It is also exclusively a North American family, as various references to questioned (Dawson, 1964; Li, 1975) or definite (Shevyreva, 1976) sciuravids from Asia have been demonstrated to be incorrect (Wood, 1977).

Although the fossil record does not show clearly the origin of the sciuravids, they are probably derived from small-sized ischyromyids near the *Franimys* group (Wilson, 1949, as "*Paramys buccatus* group") or the microparamyines (Wood, 1962). The years since 1949 have produced no more convincing ancestral stock for the "myomorphs" than the sciuravids, which tends to strengthen Wilson's position on this question. The record is especially complete for the North American derivation of the eomyids from sciuravids.

FAMILY CYLINDRODONTIDAE

Much new material of this family has been described since 1949, particularly from the late Eocene and earliest Oligocene. The earliest known cylindrodontid is still *Mysops* from the Bridgerian. *Dawsonomys woodi* of the La Barge fauna of Lost Cabinian age (Gazin, 1961) may be related to *Mysops* (W. Korth, personal communication). *Dawsonomys woodi* had previously been considered to be a sciuravid. *Mysops boskeyi* from the middle Eocene of southwest Texas (Wood, 1974) is quite similar to late Eocene *Pareumys* (Black, 1970, 1974) and may belong in that genus.

By the late Eocene a variety of cylindrodontids are known from California, Utah, and Wyoming. There are several species of *Pareumys*, with *P. guensburgi* (Black, 1970*a*) from the La Point Member of the Duchesnean River Formation in Utah, the largest and most high-crowned species of the genus. It was probably close to the ancestry of *Jaywilsonomys* of the Rancho Gaitan fauna of northeastern Chihuahua, Mexico (Ferrusquía and Wood, 1967).

A second group of cylindrodonts, also probably descended from *Mysops*, are *Pseudocylindrodon* and *Ardynomys*. *Pseudocylindrodon tobeyi* (Black, 1970*b*, 1974), known from the late Eocene, is probably not far removed from the ancestry of the Oligocene *Cylindrodon*. Both *Pseudocylindrodon* and *Cylindrodon* are known from the Porvenir fauna of the Big Bend in Texas.

FAMILY APLODONTIDAE

For many years the earliest member of the aplodontids was considered to be *Eohaplomys* of the late Eocene of California. However, recent work by Rensberger (1975) has shown that *Eohaplomys* is most probably not an aplodontid and, in fact, has nothing to do with the origins of that family. Rensberger has demonstrated a derivation of the aplodontid *Haplomys* from prosciurine rodents, a relationship earlier put forth by Matthew (1910) and McGrew (1941), and has moved the Prosciurinae from the Ischyromyidae to the Aplodontidae. *Eohaplomys* is shown to be quite different from prosciurines and is left as a specialized late Eocene ischyromyid.

Black (1971) described a new genus of rodent, *Spurimus*, from the late Eocene of Badwater, Wyoming, which he related most closely to the prosciurines. Two species of *Spurimus* occur at Badwater, one stratigraphically above and temporally later than the other. The differences between the earlier *S. selbyi* and the later *S. scotti* demonstrate reduction in the size and length of the hypolophid, in the size of the metalophid and trigonid basin, and in the size of the hypocone. This general trend would have continued from *Spurimus* into the Oligocene prosciurines. The origins of *Spurimus* within the ischyromyids are not clear but the prosciurines do not have any special relationship to either *Rapamys* or *Mytonomys* (Black, 1968*b*). Their origins are perhaps within the *Paramys delicatus* group as suggested by Wood (1962).

Uncertain Suborder
Family Protoptychidae

Study of new material of *Protoptychus* from the Washakie Basin and a reexamination of the type skull and a second facial region by Wahlert (1973) has raised some additional questions about this very enigmatic rodent. *Protoptychus,* with an enlarged infraorbital foramen and indication that the anterior part of the medial masseter passed through the foramen, is clearly hystricomorphous. The lower jaw also appears to be hystricognathous. The dentition is tetralophate with a small P^3 and molariform P^4.

This suite of characters removes the Protophychidae from the protrogomorph rodents, although an ancestry within the Ischyromyidae or Cylindrodontidae seems most probable. Whether *Protoptychus* has any special relationship to the South American Caviomorpha is unclear.

Family Eutypomyidae

In 1949 this family was known from a single Chadronian and Orellan genus, *Eutypomys.* New species of *Eutypomys* have since been described from the early Miocene of Montana (Wood and Konizeski, 1965), from the early Miocene of South Dakota (J. R. Macdonald, 1970) and from the Porvenir local fauna of Texas (Wood, 1974) but the family still remains an enigmatic one. Contrary to Wahlert (1977) there does not appear to be any close relationship between eutypomyids and castorids (Wood, 1974).

A single upper incisor from the late Eocene Candeleria local fauna of Texas was referred to the Eutypomyidae by Wood (1974:97). Dawson (1966) described *Janimus rhinophilus* from Utah, placing it with question in the Family Isehyromyidae (Paramyidae in that paper). However, she noted (1966: 106) that "a certain similarity is found between the pattern on the lower molars of *Janimus* and that of an early eutypomyid from the Chambers Tuff, Vieja Group of Texas, now being studied by A. E. Wood." Wood in his discussion of that species from the Porvenir fauna, which he named *Eutypomys inexpectatus,* stated (1974:96), "there is a distinct possibility, however, that *J. rhinophilus* is a collateral ancestor (of *Eutypomys*) and that a southern species of *Janimus* that lived during Uinta time, might have been the actual ancestor of the Eutypomyidae."

We tentatively place *Janimus* in the Eutypomyidae and follow Dawson (1966) in regarding a microparamyine ancestry for the family as most probable. She also suggested a close relationship of "*Mysops*" *kalicola* with this group.

Suborder Sciuromorpha

This suborder includes some of those rodents in which the lateral masseter has enlarged and expanded forward up the front of the zygoma and onto the snout; the infraorbital foramen is compressed into a narrow slit; and the dentition is quite similar to that of the paramyines with some specialization in more recent forms. The dental formula is 1/1, 0/0, 2-1/1, 3/3.

Family Sciuridae

No members of this family are as yet known before the early Oligocene and there is now some doubt as to whether the earliest known occurrence, ?*Protosciurus jeffersoni* (Black, 1965), should be included in the Sciuridae or removed to the Ischyromyidae. Study of the new skull and skeletal material of ?*Protosciurus jeffersoni* from Flagstaff Rim, Wyoming, demonstrates that this species was close to the actual ancestry of the Sciuridae but that it was completely protrogomorphous. The skeleton is currently under study by Richard Thorington at the National Museum of Natural History and he indicates (personal communication) that it is almost indistinguishable from that of modern *Sciurus niger.* The skull and dentition are being studied by Emry and Black and demonstrate a sciurid dentition with a protrogomorphous zygomasseteric complex.

Wood (1962) named the genus *Uriscus* based on a jaw with M_1–M_3 that was first described by Wilson (1940) from the Poway Conglomerate of California. This specimen is clearly not separable from *Reithroparamys* (Black, 1971). It seems likely that squirrels evolved during the early Oligocene through changes in their zygomasseteric structure, but retained many of the ischyromid skeletal and dental features. They certainly appear to be North American in origin.

Suborder Myomorpha

This suborder includes those rodents in which the masseter may pass up in front of the zygoma, through the zygoma, or both. The dentition is generally lophate, although occasionally it is tubercular. The dental formula is 1/1, 0/0, 1-0/1-0, 3-2/3-2.

Superfamily Geomyoidea

Only the Eomyidae are definitely known from the late Eocene with the other families, Heteromyidae and Geomyidae, appearing in the early Oligocene and late Oligocene respectively. However, as discussed later, *Griphomys* is most probably a geomyoid and the heteromyid *Heliscomys* may be present in the late Eocene. There is a great deal of new early Oligocene material referable to the Eomyidae (Black, 1965; Wood, 1974) and the Heteromyidae (Harris and Wood, 1969; Emry, 1972*a*).

Family Eomyidae

Protadjidaumo typus (Burke, 1934) was the first eomyid to be recorded from the Eocene. It was originally described from the latest Eocene, late Duchesnean La Point fauna but several undescribed species of this genus also are known to occur at Badwater (Black and Dawson, 1966). The only other eoymyid with Eocene representation is *Namatomys,* reported from the Ventura Basin of California by Lindsay (1968). Contrary to Lindsay (1968:1), "*Namatomys*" *fantasma* is probably an early specialized eomyid with no direct ancestral relationship to other muroids. Wahlert (1978) studied the cranial foramina of a variety of Oligocene members of the family and concluded that the Eomyidae cannot be ancestral to the Heteromyidae and Geomyidae but most probably share a common ancestry with them. He would include only the Heteromyidae and Geomyidae in the Geomyoidea, would raise the eomyids to superfamily rank, the Eomyoidea, and would place both superfamilies in the Infraorder Geomorpha as a sister group to an unnamed infraorder composed of the Myoxoidea, Dipodoidea, and Muroidea. While Hartenberger (1971) is probably correct in deriving the Gliridae from *Microparamys,* a common origin of dipodoids and muroids from the same stock is far less certain. In fact, cricetids and zapodids seem to be more closely related to sciuravids than to *Microparamys.* We therefore retain the Superfamily Geomyoidea for the Eomyidae, Heteromyidae, and Geomyidae, placing it in the Suborder Myomorpha. From this we remove the Gliridae (Myosoidea), leaving that group without subordinal assignment.

Suborder Castorimorpha

This suborder includes those rodents with an enlarged lateral masseter which expands in front of the zygoma, squeezing the infraorbital foramen against the snout. The cheek teeth are generally lophodont and hypsodont based upon five cross crests. The dental formula is 1/1, 0/0, 2-1/1, 3/3.

Family Castoridae

Wilson (1949:110) said ". . . the Eocene ancestors of the Castoridae have not been recognized." This is still true. Emry (1972*b*) described a new species of *Agnocastor* from the Flagstaff Rim area, referring to it as the oldest species known for the Family Castoridae. However, that material sheds no new light on the ancestry of the family and beavers are still unknown in the late Eocene. Neither are castorids represented in the early Oligocene fauna of Texas. Wood (1974:104) has suggested a possible Middle American origin for the Castoridae, but a northern center of origin separate from that of eutypomyids would seem more likely to us.

Genera of Problematic Affinities

Several genera of late Eocene rodents are impossible to assign with any confidence to a particular family. Of these, *Simimys* has been considered to be a possible cricetid (Wilson, 1949; Lindsay, 1968, 1977) or a questionable zapodid (Wood, 1974; Lillegraven and Wilson, 1975). *Griphomys,* also from the California Duchesnean, has generally been considered to be a geomyoid (Wilson, 1949; Lindsay, 1968; Lillegraven, 1977; Wood, 1980), although whether it should be a geomyid, heteromyid, or eomyid has been debated. New material of both of these genera from the late Eocene of California, the discovery of ?*Simimys* in Utah (Dawson, 1966), and of ?*Griphomys* in the earliest Oligocene along Pilgrim Creek in northwest Wyoming (Sutton and Black, 1975) has done nothing to clarify their relationships.

Of the two, the assignment of *Griphomys* to the Geomyoidea seems more secure than any familial or superfamilial allocation of *Simimys* might be. *Simimys* has been assigned to the ?Zapodidae by Lillegraven and Wilson (1975). However, as those authors note, the absence of P^4 in *Simimys* and its presence in all Tertiary zapodids poses a severe problem for this placement. Their work argues that *Simimys* should be removed from any direct relationship with cricetid or murid origins. Lindsay (1977), however, argues that *Simimys* should be considered basal to the Cricetidae.

Emry (1972*a*) and Wood (1974) have made a strong case for a close relationship among *Griphomys*; the early Oligocene heteromyid *Heliscomys,* which may already be present in the late Eocene (Dawson, personal communication); and *Meliakrouniomys,* known from the early Oligocene of

Texas. Wood places the last genus in the Eomyidae; Emry places it in the Heteromyidae. All three genera have rather simple, four-cusped, bilophate molars. *Griphomys toltecus* has perhaps the most primitive molar morphology of the three genera, retaining a mesoconid-mesolophid structure not present in *Meliakrouniomys* and *Heliscomys*. Lillegraven (1977: 248) refers to a new and distinct genus of rodent very similar to material called "*Namatomys*" *fantasma* (Lindsay, 1968) as being possibly close to the ancestry of *Griphomys*. Another genus which may belong in this early geomyoid group is *Floresomys* from beds of perhaps late Eocene or early Oligocene-age near Guanajuato, Mexico (Fries et al., 1955; Black and Stephens, 1973). *Floresomys* was initially assigned to the Sciuravinae (Sciuravidae) but it is quite different from other sciuravids in having basically bilophate molars with no protocone/hypocone or protoconid/hypoconid connection. $P^4/_4$ are reduced over those of sciuravids and are closer to those of heteromyids than sciuravids. The ancestry of this geomyoid complex may ultimately be found in the Sciuravidae close to a form such as *Pauromys* (Dawson, 1968).

Two other genera, *Prolapsus* (Wood, 1973) and *Guanajuatomys* (Black and Stephens, 1973), also defy familial placement at the present time. Both are hystricognathous although they differ from each other in all other respects, including their mode of hystricognathy. In *Prolapsus,* the angle arises lateral and ventral to the incisor alveolus, while in *Guanajuatomys* the angle arises lateral and dorsal to the incisor alveolus. The cheek teeth also differ morphologically; those of *Prolapsus* are sciuravid-like whereas those of *Guanajuatomys* are more similar to ischyromyids. Those two genera and *Protoptychus* suggest an early and heretofore unknown radiation of hystricognathous rodents in North America. This hystricognathy is totally removed from the so-called incipient hystricognathy (Wood, 1962:117) of *Reithroparamys,* a condition we cannot find in numerous jaws of that genus that we have examined.

Wood (1974:102) has proposed the possible existence of a distinctive rodent fauna in Central America during the Eocene, from which the Caviomorpha of South America may have evolved together with the problematic *Simimys, Griphomys, Floresomys, Prolapsus,* and *Guanajuatomys* and several of the early Oligocene genera found in Texas. He suggests that their presence in Mexico, Southern California, and Texas represents a northern migration from this Middle American center.

The concept has a certain appeal, particularly as it suggests a place of origin for the Geomyoidea in the middle Eocene to early late Eocene, with a rather rapid spread northward. *Floresomys, Griphomys,* and *Meliakrouniomys* could well be a part of this early diversification. *Simimys* could represent an early development of the cricetid-like dentition, together with the early Oligocene cricetid *Nonomys* (Emry and Dawson, 1972), known from the Flagstaff Rim area of central Wyoming. Emry and Dawson (1972:10) describe *Nonomys* as having a greater similarity to later hesperomyine cricetids than to the eumyine Oligocene members of the family. Others have suggested (Black, 1964; Patterson and Pascual, 1972:294–296) a Middle American center of origin for the hesperomyine cricetids, which invaded South America at the end of the Pliocene. *Simimys* and *Nonomys* may represent northern immigrants of an early group of rodents that developed reduced dentitions with simplified cricetid-like morphologies from sciuravids in such a Central American center. This would suggest that the New World Hesperomyinae (Cricetidae) have a much longer and more isolated history than previously supposed. The great variety of hesperomyines, some 40 genera in South America today, may also indicate a long history of diversification for the subfamily.

CONCLUSIONS

1. The details of the origin of rodents are no clearer today than in 1949.

2. As many genera of early Tertiary North American rodents have been described since 1949 as were known at that time.

3. It still appears likely that all rodents differentiated from a protrogomorphous paramyine ischyromyid stock.

4. The sciuromorphous, myomorphous, and hystricomorphous zygomasseteric complexes evolved several times independently.

5. There is some evidence for a Central American radiation of myomorph rodents from sciuravids, and for a subsequent spread northward of eomyids and cricetids late in the Eocene.

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LITERATURE CITED

Black, C. C. 1964. *Review of* Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phylotine groups. J. Paleont., 38:611–612.

———. 1965. Fossil mammals from Montana. Pt. 2. Rodents from the early Oligocene Pipestone Springs local fauna. Ann. Carnegie Mus., 38:1–48.

———. 1968*a*. The Oligocene rodent *Ischyromys* and discussion of the Family Ischyromyidae. Ann. Carnegie Mus., 39: 273–305.

———. 1968*b*. The Uintan rodent *Mytonomys*. J. Paleont., 42: 853–856.

———. 1970*a*. A new *Pareumys* (Rodentia: Cylindrodontidae) from the Duchesne River Formation, Utah. Field Mus. Nat. Hist., Fieldiana Geol., 16:453–459.

———. 1970*b*. Paleontology and geology of the Badwater Creek area, central Wyoming. Pt. 5. The cylindrodont rodents. Ann. Carnegie Mus., 41:201–214.

———. 1971. Paleontology and geology of the Badwater Creek area, central Wyoming. Pt. 7. Rodents of the Family Ischyromyidae. Ann. Carnegie Mus., 43:179–217.

———. 1974. Paleontology and geology of the Badwater Creek area, central Wyoming. Pt. 9. Additions to the cylindrodont rodents from the late Eocene. Ann. Carnegie Mus., 45:151–160.

Black, C. C., and M. R. Dawson. 1966. A review of late Eocene mammalian faunas from North America. Amer. J. Sci., 164: 321–349.

Black, C. C., and J. R. Stephens III. 1973. Rodents from the Paleogene of Guanajuato, Mexico. Occ. Papers, Texas Tech Univ. Mus., 14:1–10.

Bowen, T. M. 1979. Geology and paleontology of the Sand Creek facies, lower Willwood Formation (Lower Eocene), Washakie County, Wyoming. Mem. Geol. Surv. Wyoming, 2:31–151.

Bugge, J. 1974. The cephalie arterial system in insectivores, primates, rodents and lagomorphs with special reference to the systematic classification. Acta Anatomica, 87 (Supplement 62):1–160.

Burke, J. J. 1934. New Duchesne River rodents and a preliminary survey of the Adjidaumidae. Ann. Carnegie Mus., 23: 391–398.

Dawson, M. R. 1961. The skull of *Sciuravus nitidus*, a middle Eocene rodent. Postilla, 53:1–13.

———. 1962. A sciuravid rodent from the middle Eocene of Wyoming. Amer. Mus. Novit., 2075:1–5.

———. 1964. Late Eocene rodents (Mammalia) from Inner Mongolia. Amer. Mus. Novit., 2191:1–15.

———. 1966. Additional late Eocene rodents (Mammalia) from the Uinta Basin, Utah. Ann. Carnegie Mus., 38:97–114.

———. 1968. Middle Eocene rodents (Mammalia) from northeastern Utah. Ann. Carnegie Mus., 39:327–370.

———. 1974. Paleontology and geology of the Badwater Creek area, central Wyoming. Pt. 8. The rodent *Microparamys* (Mammalia). Ann. Carnegie Mus., 45:145–150.

Emry, R. J. 1972*a*. A new heteromyid rodent from the early Oligocene of Natrona County, Wyoming. Proc. Biol. Soc. Washington, 85:179–190.

———. 1972*b*. A new species of *Agnotocastor* (Rodentia, Castoridae) from the early Oligocene of Wyoming. Amer. Mus. Novit., 2485:1–7.

Emry, R. J., and M. R. Dawson. 1972. A unique cricetid (Rodentia, Mammalia) from the early Oligocene of Natrona County, Wyoming. Amer. Mus. Novit., 2508:1–14.

Ferrusquía-Villafranca, I., and A. E. Wood. 1967. New fossil rodents from the Rancho Gaitan local fauna, northeastern Chihuahua, Mexico. Pearce Sellars Series, Texas Mem. Mus., 16:1–3.

Fries, C., C. W. Hibbard, and D. H. Dunkle. 1955. Early Cenozoic vertebrates in the red conglomerate at Guanajuato, Mexico. Smithsonian Misc. Coll., 123(7):1–25.

Gazin, C. L. 1961. New sciuravid rodents from the Lower Eocene Knight Formation of western Wyoming. Proc. Biol. Soc. Washington, 74:193–194.

———. 1962. A further study of the Lower Eocene mammalian faunas of southwestern Wyoming. Smithsonian Misc. Coll., 144(1):1–98.

Golz, D. I., and J. A. Lillegraven. 1977. Summary of known occurrences of terrestrial vertebrates from Eocene strata of southern California. U. Wyoming, Contrib. Geol., 15:43–65.

Guthrie, D. A. 1963. The carotid circulation in the Rodentia. Bull. Mus. Comp. Zool., Harvard Univ., 128:455–481.

———. 1967. The mammalian fauna of the Lysite Member, Wind River Formation (early Eocene) of Wyoming. Mem. S. California Acad. Sci., 5:1–53.

———. 1971. The mammalian fauna of the Lost Cabin Member, Wind River Formation (Lower Eocene) of Wyoming. Ann. Carnegie Mus., 43:47–113.

Harris, J. M., and A. E. Wood. 1969. A new genus of eomyid rodent from the Oligocene Ash Spring local fauna of Trans Pecos Texas. Pearce Sellards Series, Texas Mem. Mus., 14: 1–7.

Hartenberger, J.-L. 1971. Contribution à l'étude des genres *Gliravus* et *Microparamys* (Rodentia) de l'Éocene d'Europe. Palaeovertebrata, 46:97–135.

Li, C.-k. 1975. *Yuomys*, a new ischyromyoid rodent genus from the Upper Eocene of north China. Vert. Palasiatica, 13:58–70.

———. 1977. Paleocene eurymyloids (Anagalida, Mammalia) of Gianshan, Anhi. Vert. Palasiatica, 15:116–118.

———. 1977. *Simimys* and origin of the Cricetidae (Rodentia: Muroidea). Geobios, 10:597–623.

LILLEGRAVEN, J. A. 1977. Small rodents (Mammalia) from Eocene deposits of San Diego County, California. Bull. Amer. Mus. Nat. Hist., 158:222–261.

LILLEGRAVEN, J. A., and R. W. WILSON. 1975. Analysis of *Simimys simplex*, an Eocene rodent (?Zapolidae). J. Paleont., 49: 856–874.

LINDSAY, E. 1968. Rodents from the Hartman Ranch local fauna, California. Paleo. Bios., Univ. California Mus. Paleont., 6:1–22.

———. 1977. *Simimys* and the origin of the Cricetidae (Rodentia: Muroidea). Geobios, 10:597–626.

MACDONALD, J. R. 1970. Review of the Miocene Wounded Knee faunas of southwestern South Dakota. Bull. Sci., Los Angeles Co. Mus. Nat. Hist., 8:1–82.

MATTHEW, W. D. 1910. On the osteology and relationships of *Paramys* and the affinities of the Ischyromyidae. Bull. Amer. Mus. Nat. Hist., 28:43–71.

MCGREW, P. O. 1941. The Aplodontoidea. Field Mus. Nat. Hist., Fieldiana Geol., 9:1–30.

MCKENNA, M. C. 1961. A note on the origin of rodents. Amer. Mus. Novit., 2037:1–5.

———. 1975. Toward a phylogenetic classification of the Mammalia. Pp. 21–46, *in* Phylogeny of the primates (W. P. Ludsett and F. S. Szalay, eds.). Plenum Publ. Co., New York.

PATTERSON, B., and R. PASCUAL. 1972. The fossil mammal fauna of South America. Pp. 247–309, *in* Evolution mammals and southern continents (A. Keast, F. C. Erk, and B. Glass, eds.). State Univ. New York Press, Albany.

RENSBERGER, J. M. 1975. *Haplomys* and its bearing on the origin of the aplodontoid rodents. J. Mamm., 56:1–14.

SHEVYREVA, N. S. 1976. Paleogene rodents of Asia. Trans. Paleont. Inst., Acad. Sci. USSR, 158:10115.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., 85: i–xvi + 1–350.

STEHLIN, H. G., and S. SCHAUB. 1951. Die Frigono dontie der simplicidentoten Nager, Schweizerischen Palidont. Abhandl., 67:1–385.

SUTTON, J. F., and C. C. BLACK. 1975. Paleontology of the earliest Oligocene deposits in Jackson Hole, Wyoming. Pt. 1. Rodents exclusive of the Family Eomyidae. Ann. Carnegie Mus., 45:299–315.

SZALAY, F. S., and R. L. DECKER. 1974. Origins, evolution, and function of the tarsus in late Cretaceous Eutheria and Paleocene primates. Pp. 223–259, *in* Primate locomotion (F. A. Jenkins, Jr., ed.). Academic Press, New York.

WAHLERT, J. H. 1968. Variability of rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and recent rodent groups. Breviora, 309:1–18.

———. 1973. *Protoptychus*, a hystricomorphous rodent from the late Eocene of North America. Breviora, 419:1–14.

———. 1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. Bull. Mus. Comp. Zool., Harvard Univ., 146:363–410.

———. 1977. Cranial foramina and relationship of *Eutypomys* (Rodentia, Eutypomyidae). Amer. Mus. Novit., 2626:1–8.

———. 1978. Cranial foramina and relationship of the Eomyoidea (Rodentia, Geomorpha). Skull and upper teeth of *Kansasimys*. Amer. Mus. Novit., 2645:1–16.

WEST, R. M. 1973. Geology and mammalian paleontology of the New Fork-Big Sandy area, Sublette County, Wyoming. Field Mus. Nat. Hist., Fieldiana Geol., 19:1–193.

WILSON, J. A. 1978. Stratigraphic occurrence and correlation of early Tertiary vertebrate faunas. Trans Pecos Texas. Pt. 1. Vieja area. Bull. Texas Mem. Mus., 25:1–42.

WILSON, R. W. 1940. California paramyid rodents. Carnegie Inst. Washington, Contrib. Paleont., 514:59–83.

———. 1949. Early Tertiary rodents of North America. Carnegie Inst. Washington, Contrib. Paleont., 584:67–164.

WOOD, A. E. 1955. A revised classification of the rodents. J. Mamm., 36:165–187.

———. 1956. *Mytonomys*, a new genus of paramyid rodent from the Upper Eocene. J. Paleont., 30:753–755.

———. 1959*a*. A new sciuravid rodent of the genus *Pauromys* from the Eocene of Wyoming. Amer. Mus. Novit., 1978: 1–6.

———. 1959*b*. Rodentia. *In* The geology and paleontology of the Elk Mountain and Tabernacle Butte area, Wyoming. Bull. Amer. Mus. Nat. Hist., 117:157–169.

———. 1962. The early Tertiary rodents of the Family Paramyidae. Trans. Amer. Phil. Soc., n.s., 52:1–261.

———. 1965. Small rodents from the early Eocene Lysite Member, Wind River Formation of Wyoming. J. Paleont., 39: 124–134.

———. 1973. Eocene rodents Pruett Formation, southwest Texas; their pertinence to the origin of the South American Caviomorpha. Pearce Sellards Series, Texas Mem. Mus., 20: 1–40.

———. 1974. Early Tertiary vertebrate faunas Vieja Group Trans Pecos Texas: Rodentia. Bull. Texas Mem. Mus., 21: 1–112.

———. 1976. The Oligocene rodents *Ischyromys* and *Titanotheriomys* and the content of the Family Ischyromyidae. Royal Ontario Mus. Life Sci., Misc. Publ.:244–277.

———. 1977. The evolution of the rodent Family Ctenodactylidae. J. Paleont. Soe. India, 20:120–137.

———. 1980. The Oligocene rodents of North America. Trans. Amer. Phil. Soc., 70(5):1–68.

WOOD, A. E., and R. L. KONIZESKI. 1965. A new eutypomyid rodent from the Aarikanean (Miocene) of Montana. J. Paleont., 39:492–496.

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ON *MESOGAULUS PANIENSIS* (RODENTIA) FROM HEMINGFORDIAN (MIDDLE MIOCENE) DEPOSITS IN NORTHEASTERN COLORADO

Edwin C. Galbreath

ABSTRACT

Previously undescribed cranial, dental, and postcranial specimens of *Mesogaulus paniensis* from the middle Miocene of Quarry A, Martin Canyon, northeastern Colorado, contribute to understanding the morphology and phylogeny of this rodent. Features of P_4 suggest that *M. paniensis* is in a line approaching *Mylagaulus*. The Mylagaulidae may be more diverse taxonomically than had been recognized.

INTRODUCTION

W. D. Matthew (1902) named and described *Mylagaulus paniensis* on the basis of a fragment of lower jaw with the fourth premolar and the anterior end of the incisor. Cook and Gregory (1941) assigned the species to the genus *Mesogaulus*. Wilson (1960) published a detailed analysis of specimens from the Martin Canyon Local Fauna (Galbreath, 1953) that have been assigned to *Mesogaulus paniensis*. Following is new information concerning *Mesogaulus paniensis* from the Quarry A area of Martin Canyon. KU specimen numbers refer to material in the Museum of Natural History, University of Kansas, Lawrence. This list of specimens represents innumerable hours of searching conducted in almost every year since 1956. While specimens were found only in the Quarry A area, the search covered other parts of Martin Canyon and other deposits in Logan County containing the Martin Canyon Local Fauna.

DESCRIPTION OF SPECIMENS

Snout and mandible; KU 160; Fig. 1A and 1B.—So far as I know, Fig. 1A and 1B provide the only known illustration of the snout and mandible discussed by Wilson. Photographs presented to me by H. H. Lane were used to make this illustration.

Since commenting on this specimen in 1953, I am more convinced than I was then that KU 160 was collected by H. T. Martin in 1925 in the area of Quarry A, where most of the Martin Canyon Local Fauna was found. Undoubtedly Martin was acquainted with the wealth of exposed fragments at the site of the future Quarry A, since he was a member of the American Museum Expedition that visited the area in 1898.

Central part of skull; KU 47268; Fig. 1C, D, and E.—This fragment of the skull is notable for the fine preservation of the cheek teeth, including ample evidence of cement covering the crowns, infraorbital canal, and frontal bone. The frontal bone was in close association with but not actually united to the principal part of the specimen. The P^3 nestles in the antero-internal concavity of P^4 with the tip slightly curved posteriorly.

Dimensions of the parts are presented in an appendix.

Part of frontals and parietals; KU 55301; Fig. 2A.—These fragments of the skull roof show the temporal crests uniting to form the sagittal crest, which extends posteriorly to the lambdoidal crest. There is no way to determine the development of the lambdoidal crest but presumably it was weak like the sagittal crest. The space between these fragments in the illustration is a minimal estimation based on the probable curve of the temporal crests.

Small parts of the zygomatic arches found in association with the frontals and parietals indicate that the arch was strong and mylagaulid-like.

Dimensions of the skull roof fragments are indicated in Fig. 2A.

Fourth upper premolar.—A damaged upper premolar of *Mesogaulus paniensis* shows that the buccal arm separated from the anterofossette about 5.5

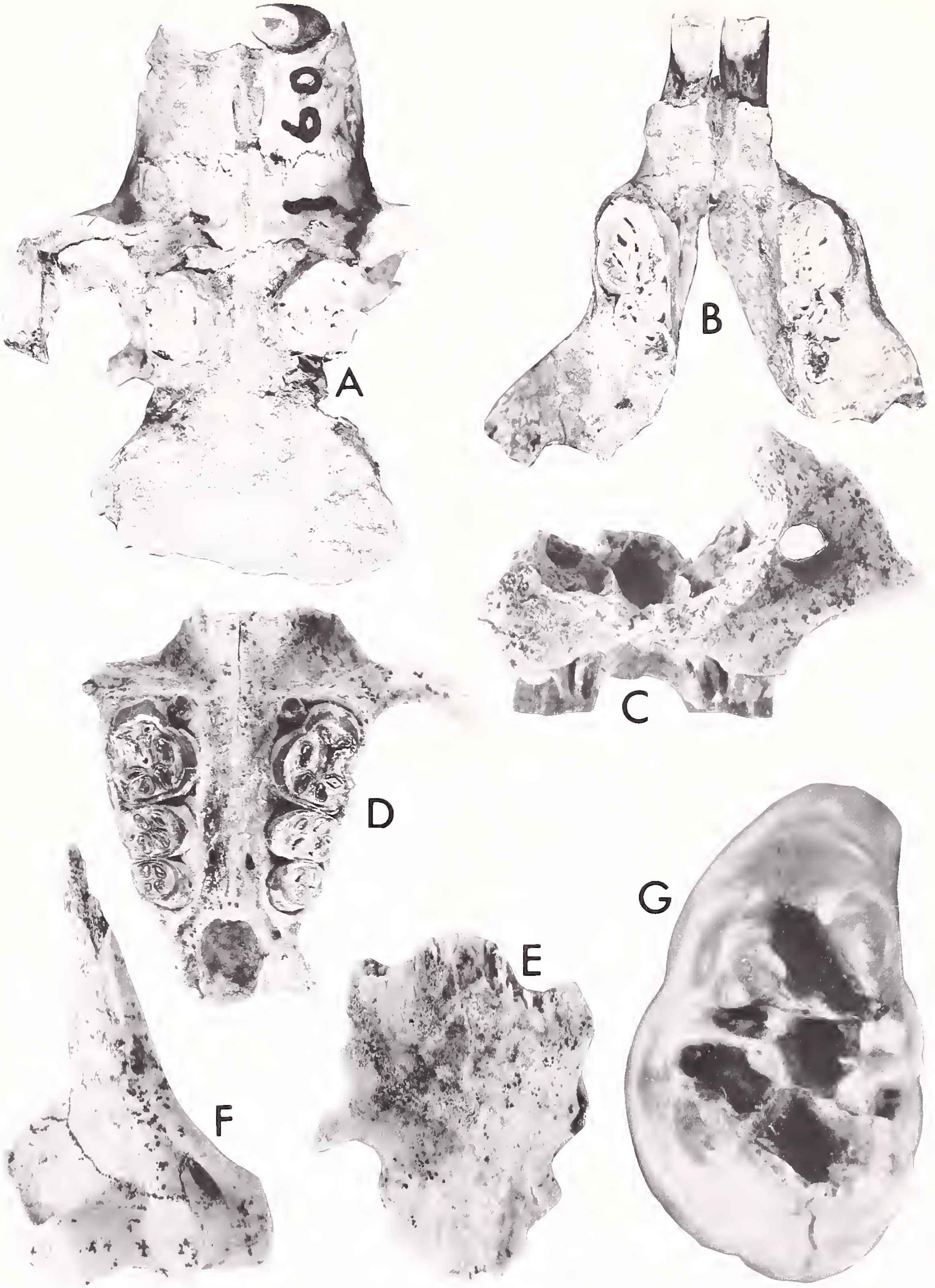

Fig. 1.—*Mesogaulus paniensis* (Matthew). A: ventral view of anterior part of the skull, KU 160. B: dorsal view of lower jaws, KU 160. C: anterior view of skull fragment. D: palatal view of skull fragment. E: dorsal view of associated fragment of frontal bone, all KU 47268. F: distal end of right humerus, KU 55303. G: left P_4, KU 55302. The mottled light and dark coloration of this specimen causes a deceptive view of the occlusal surface.

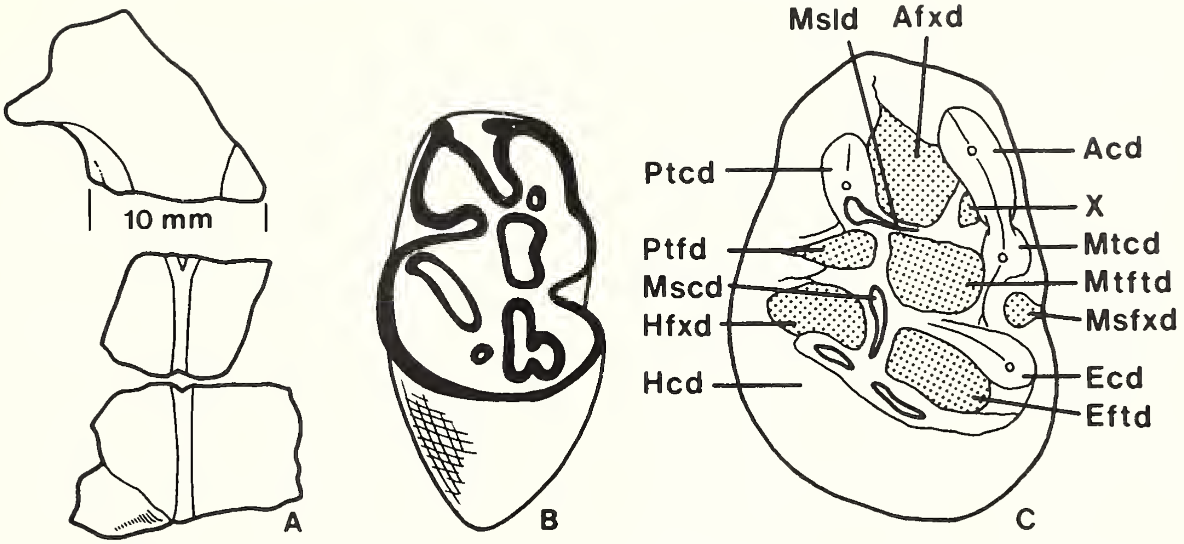

Fig. 2.—*Mesogaulus paniensis* (Matthew). A: fragments of frontal and parietal bones, KU 55301. B: left P_4, KU 9364 (from Galbreath, 1953, fig. 24). C: left P_4, KU 55302.

mm above the base of the crown and continued as a separate fossette to the base of the crown. This separation is consistent with Cook and Gregory's report (1941) on *Mesogaulus praecursor* but certainly unlike the separation of the lingual arm from the "Y" reported by Black and Wood (1956) for *Mesogaulus novellus.*

The P^4 has two strong inner roots (the posterior being dominant) and a small postero-external root. The tips of the roots curve outward and in the case of the postero-external root the tip causes a bulge on the lateral wall of the maxillary.

Fourth lower premolar; KU 55302; Fig. 1G and 2C.—Probably the most interesting specimen of *Mesogaulus paniensis* from Martin Canyon is a virtually unworn left P_4. The crown has seven fossae. Its occlusal surface is a "plateau" with metalophulid, mesoconid, and ectolophid well developed; metafossettid and entofossettid completely enclosed; and anteroflexid, protoflexid, hypoflexid, and a lingual invagination (mesoflexid of *Mylagaulus*) almost closed. Bordering this plateau with its deep fossae are the anteroconid, metaconid, entoconid, and hypoconid "hills." Although Fig. 1G does not show it, deep (1.5 mm) in the cavity of the anteroflexid one can see the spur projecting from the metalophulid to the anteroconid, forming the small fossettid (Fig. 2C), which appears as a "lakelet" after wear (Fig. 2B). It is beyond the evidence of this one tooth to determine whether the spur developed to cut off part of the anteroflexid or if this fossettid is the result of an earlier invagination between the anteroconid and metaconid. The "lingual invagination" has part of the external wall damaged (Fig. 2C) but it too must have had a narrow-mouthed "valley" opening. Probing this fossa shows this invagination to be a deep fossettid that may have joined with the entoconid—an impression in keeping with the outline of the entofossettid in Fig. 2B.

This specimen has a pattern closely similar to the one unworn P_4 of *Mylagaulus laevis* (Kennesaw Local Fauna, northeast Colorado) that I have seen. The principal differences are those of proportion: *Mylagaulus laevis* has a small metafossettid and a long mesoflexid.

Dimensions of this tooth are presented in the Appendix.

Distal end of humerus; KU 55303; Fig. 1F.—This damaged distal end of a humerus shows that *Mesogaulus paniensis* had developed the burrowing specialization equal to that of the later mylagaulids.

Dimensions of the fragment are presented in the Appendix.

REMARKS

Combining the measurements of the various specimens, I estimate that the skull and skeleton of *Mesogaulus paniensis* was about three quarters of the size of *Mylagaulus laevis*. Certainly the unworn P_4 of *Mesogaulus paniensis* shows a complicated pattern that is not matched by other mesogaulids. With the material at hand I think that *Mesogaulus paniensis* was more like *Mylagaulus* than was once realized.

The upper and lower premolars of *Mesogaulus paniensis* and *Mesogaulus praecursor* offer some basis for speculation about *Mesogaulus novellus* (Matthew). Black and Wood (1956:684) considered the possibility that *Mesogaulus novellus* might be a side line off the main evolutionary history of the genus. Concerning *Mesogaulus novellus*, these authors commented on the separation of the lingual arm from the Y fossette of P^4 with wear and associated the anterconid of P_4 with the buccal side of the tooth. These features are the reverse of the condition found in *Mesogaulus paniensis* and *Mesogaulus praecursor*. If these differences prove to be reliable, *Mesogaulus novellus* might better be placed in a new genus.

The terminology of occlusal structures of the mylagaulid premolars is of special interest. Wood and Wilson (1936) presented a nomenclature for teeth of rodents that is sound. Admittedly, it is not easy to use in working with worn teeth of mylagaulids unless one understands the development of the teeth. I think McGrew's (1941:20) use of "invagination" to explain the origin of some fossettes and fossettids is useful. The invaginations had their origin in the enamel margins and became part of the crowns. In *Mesogaulus paniensis* I have interpreted the metafossettid as an invagination that was followed by a second invagination, the mesoflexid, which encroached on and closed off the metaflexid and made it a metafossettid. In the unworn P_4 of *Mylagaulus laevis* referred to above, the encroachment resulted in a reduced metafossettid and an elongate mesoflexid.

I am mindful of the problems that these premolars present. Comments on variability preface most discussions about the teeth of the mylagaulids. Variability should be evaluated with regard to which "variations" are differences between species, and which are variations occurring within species. Variations of occlusal patterns within a species are intimately associated with development of the crowns of the teeth but how often will studies of such development be possible? In this paper I have placed a high value on the pristine crowns of *Mesogaulus paniensis*, *Mesogaulus praecursor*, and *Mesogaulus novellus*. Probably this is justified since the fourth premolars are the dominant cheek teeth.

I suspect there are more species than are recognized in the Mylagaulidae and, if so, I think the failure to recognize systematic diversity owes to lack of material and a tendency to oversimplify evolution in the Mylagaulidae. A case in point is the reference of Barstovian and Hemphillian material to the *laevis* and *monodon* entities respectively regardless of the incompatibility of some of the occlusal patterns or geographic locations—Webb (1966: 410) cited a good analogy of this problem of geographic locality with his reference to the specialized burrowing geomyids. If the unworn crowns and subsequent occlusal patterns are of taxonomic value, then I realize that these remarks practically commit me to regard *Mylagaulus douglassi* McKenna and *Mylagaulus kinseyi* Webb, with their additional distinctive features, as two different genera.

The comments I have presented should be regarded as a speculative exploration of what the features of the premolars might signify. My tenets are: (1) the diversity of the burrowing geomyids suggests that a similar diversity could have occurred in the Mylagaulidae; (2) changes in the occlusal pattern of a tooth are initiated in the formation of the tip of the tooth (the first part to be formed) and those changes with a positive selection value, more triturating surface in the P_4 in this case, are subsequently incorporated into the crown of the tooth; and (3) separation of the lingual arm from the "Y" of P^4 and the association of the anteroconid with the buccal side of P_4 are a combination of features of taxonomic value that separate *Mesogaulus novellus* from *Mesogaulus paniensis* and *Mesogaulus praecursor* where the buccal arm separates from the "Y" in P^4 and the anteroconid is associated with the lingual side in P_4.

Consequently, I think there are lines of evolutionary diversity in the mesogaulids and mylagaulids and that the P_4 indicates that *Mesogaulus paniensis* was in a line showing an approach to the condition seen in *Mylagaulus*.

LITERATURE CITED

Black, C. C., and A. E. Wood. 1956. Variation and tooth-replacement in a Miocene mylagaulid rodent. J. Paleont., 30:672–684.

Cook, H. J., and J. T. Gregory. 1941. *Mesogaulus praecursor,* a new rodent from the Miocene of Nebraska. J. Paleont., 15: 549–522.

Galbreath, E. C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. Univ. Kansas Paleont. Contr., Vertebrata, art. 4:1–120.

McGrew, P. O. 1941. The Aplodontoidea. Geol. Ser., Field Mus. Nat. Hist., 9:1–30.

Matthew, W. D. 1902. A horned rodent from the Colorado Miocene. With a revision of the Mylagauli, beavers, and hares of the American Tertiary. Bull. Amer. Mus. Nat. Hist., 16:291–310.

Webb, S. D. 1966. A relict species of the burrowing rodent, *Mylagaulus,* from the Pliocene of Florida. J. Mamm., 47: 401–412.

Wilson, R. W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. Univ. Kansas Paleont. Contr., Vertebrata, art. 7:1–92.

Wood, A. E., and R. W. Wilson. 1936. A suggested nomenclature for the cusps of the cheek teeth of rodents. J. Paleont., 10:388–391.

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APPENDIX

Dimensions of specimens of *Mesogaulus paniensis* in millimeters

Anterior end of skull, KU 160 (Fig. 1A–B).—See Wilson, 1960.

Palate and frontal bone, KU 47268 (Fig. 1C–E).—P^4–M^3 length at alveolar border: R 13.40; L 14.40. P^4–M^3 length at occlusal surface: R 12.30; L 12.35. P^3 ap and tr dimensions at base: R & L; 1.7, 1.5. P^4 ap and tr occlusal dimensions: R 6.10, 5.03; L 6.25, 5.02. P^4 ap and tr alveolar dimensions: R 6.98, 5.41; L 7.10, 5.44. P^4 height, occlusal surface to tip of postero-internal root: 10.39. M^2 ap and tr occlusal dimensions: R 3.40, 4.55; L 3.15, 4.19. M^2 estimated height from occlusal surface to tip of root: <4.00. M^3 ap and tr occlusal dimensions: R 2.80, 3.06; L 2.80, 3.25. Width of external borders of alveoli at P^4: 17.32. Width of external borders of alveoli at M^3: 11.20. Width from midline to lateral edge of zygoma: 17.20. Length of postorbital process: 3.85.

Left P_4, KU 55302 (Figs. 1G and 2C).—Ap and tr dimensions of tip of crown: 5.20, 3.50. Greatest ap and tr dimensions of crown: 8.20, 4.60. Height of greatest ap and tr dimensions from base of crown: 3.50. Greatest height of crown: 10.40. Estimated height of crown plus roots: 12.5.

Distal end of humerus, KU 55303 (Fig. 1F).—Width of damaged distal end: 14.60, estimated width 17.00.

A SURVEY OF TERTIARY SPECIES OF *PEROGNATHUS* (PEROGNATHINAE) AND A DESCRIPTION OF A NEW GENUS OF HETEROMYINAE

James E. Martin

ABSTRACT

During investigation of the sediments and rodent faunas of the Hemphillian (Miocene) of northern Oregon, two new species of pocket mice were collected. The smaller is a perognathine, *Perognathus stevei* new species, and appears to be closely related to the extant species, *P. parvus*. The second new taxon, *Oregonomys* new genus, is a heteromyine whose morphology parallels that of *Dipodomys* and includes the species: *O. pebblespringsensis* new species, *O. sargenti*, and *O. magnus*. The latter two species were previously regarded as large species of *Perognathus*. A phylogenetic line can be traced from *O. pebblespringsensis* to *O. magnus* on the basis of morphological features and stratigraphic position.

INTRODUCTION

Since R. W. Wilson's (1937) review of the Hemphillian rodents, only J. A. Shotwell (1956, 1970) has added extensively to the knowledge of rodent faunas in the Northwest. My interest in the faunas of northern Oregon came through collections made by Willis Fry. As an associate of the Burke Museum at the University of Washington, Fry collected many specimens from the Ordnance (Westend Blowout) locality, including a few complete *Spermophilus* and *Hypolagus* dentaries. From this and other localities across northern Oregon (Fig. 1), I assembled one of the largest collections of Hemphillian rodents on the West Coast. The sample is large enough to demonstrate intraspecific variation for most taxa, including the pocket mice discussed in this contribution.

Geological observations and collections of vertebrate fossils were obtained from three regions in northern Oregon from sediments assigned to the Dalles Formation by Newcomb (1966, 1971) and considered to be of Hemphillian age (Shotwell, 1956, 1958). The Ordnance locality, which lies about 10 miles south of the Columbia River, no longer exists as a source of fossil vertebrates. It has been cultivated by Saber Farms, Inc., who graciously allowed me to collect before the area was destroyed. The collection made from this square-mile blowout is of immense proportions. Although a fauna from McKay Reservoir, the second area collected, had been described (Shotwell, 1956), the additional specimens collected provide increased knowledge of the morphology of described species, add new elements to the fauna, and give a better indication of the age and environment represented. These specimens were found in siltstones and sandstones on the eastern edge of McKay Reservoir, south of Pendleton, Oregon, from about 500 ft of lateral exposure. The vertical distribution is somewhat limited, but fossils have been found in place from the upper 50 ft. The third region, south of Arlington, Oregon, consists of numerous localities in a small geographical area. From about 10 square mi on the Henry Krebs Ranch, 12 localities produced fossil mammals described in this report. Of these, 3 have been described previously: Kreb's Ranch I, University of Oregon locality 3222; Kreb's Ranch II, University of Oregon locality 2323, and California Institute of Technology locality 375 (Shotwell, 1958; Hutchison, 1968). All 12 localities (Arlington 3–15) were stratigraphically collected from a section with 3 successive units: a conglomerate layer, a buff sandstone and siltstone unit, and a red siltstone capped by a caliche layer. Only one locality, Arlington 15 (Kreb's Ranch I) overlies the caliche layer by approximately 50 ft, and one locality, Arlington 13, is a reworked Pleistocene sandstone below the conglomerate layer. Although the specimens from this latter locality cannot be used for biostratigraphic analysis and synthesis, their structures are identical to those from the upper units, and can therefore be used for their additional morphological data.

Of the two genera described herein, this is the first report of *Perognathus* from Ordnance and Arlington. Shotwell (1956) mentioned a few fragmentary specimens from McKay Reservoir. From this locality, he also described a large species with a brachyodont dentition, *Perognathus sargenti*, and Zakrzewski (1969) named *Perognathus magnus* from the Hagerman fauna in Idaho. Collections from McKay Reservoir have produced additional speci-

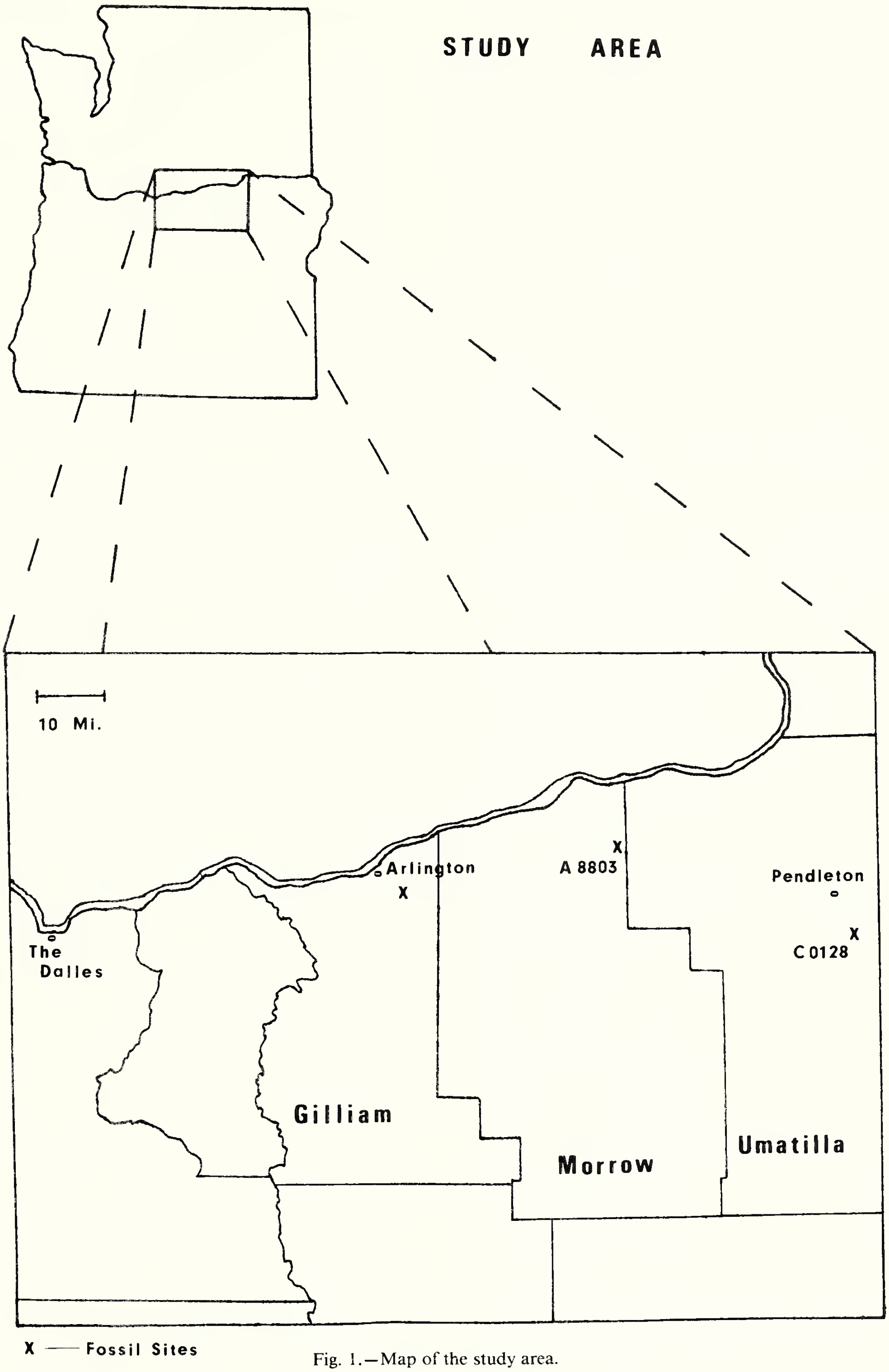

Fig. 1.—Map of the study area.

mens of *P. sargenti,* and Philip Bjork collected a well preserved dentary of *P. magnus* from Hagerman. These additional specimens indicate the occurrence of two genera of pocket mice at each locality: *Perognathus sensu stricto* and *Oregonomys* new genus. The latter genus includes the large species from Arlington and Ordnance, *O. pebblespringsensis* new species, the species from McKay Reservoir, *O. sargenti,* and that from Hagerman, *O. magnus.*

All measurements are in mm and probabilities were calculated by using the Fisher 2 × 2 contingency tables (See Rensberger, 1971).

Abbreviations—Morphological and Statistical: AP, anteroposterior measurement; CV, coefficient of variation; N, number of specimens; OR, observed range; S, standard deviation; T, transverse measurement; $\bar{X}$, mean.

Abbreviations—Institutional: MCZ, Museum of Comparative Zoology, Harvard; SDSM, South Dakota School of Mines & Technology; UALP, University of Arizona, Laboratory of Paleontology; UMMP, University of Michigan, Museum of Paleontology; UO, University of Oregon; UWBM, University of Washington, Burke Museum.

ACKNOWLEDGMENTS

I thank Mr. and Mrs. Henry Krebs for access to their property near Arlington and to Saber Farms, Inc. for entry into the Ordnance locality. Howard Coombs, University of Washington, enthusiastically encouraged the project, and with Ray Halicki of Portland General Electric Company granted permission to collect at some Arlington localities. I thank the late Willis Fry, who initiated the field investigations, and Mr. and Mrs. Ben Witte and W. Steve Nelson and family for their dedicated assistance in the field and laboratory. I am grateful to V. S. Mallory, Robert M. Mengel, Charles A. Repenning, John M. Rensberger, and Harry Wheeler who provided invaluable suggestions and reviewed the manuscript. I am indebted to Gerald Smith at the University of Michigan, Museum of Paleontology, Philip Bjork at the Museum of Geology at the South Dakota School of Mines and Technology, and Eric Gustafson at the University of Oregon for allowing me to inspect specimens from their collections. Judy Frostega did the darkroom work for the plates, and Nancy Williams and Kathy Streeter prepared the illustrations.

Most of all, I thank Robert W. Wilson, who inspired me to start and continue my career in vertebrate paleontology. His professionalism, congeniality, and expertise provide all scientists with an unparalleled example.

SYSTEMATIC PALEONTOLOGY

Geomyidae Gill, 1872
Perognathinae Wood, 1935
Perognathus Maximilian, 1839

Perognathus stevei, new species

Holotype.—UWBM 57153, maxillary with P^4–M^2.

Type locality.—Ordnance locality (A8803).

Stratigraphic position.—Dalles Formation, *sensu lato* (Newcomb, 1971).

Age.—Hemphillian.

Referred specimens.—UWBM 57150, 40 upper incisors; UWBM 57151, rostrum (edentulous); UWBM 57152, maxillary with P^4–M^2; UWBM 57154, maxillary with P^4–M^1; UWBM 57155–57156, maxillaries with P^4; UWBM 57157–57160, maxillaries with M^1–M^2; UWBM 57161, M^1; UWBM 57162, M^2; UWBM 57163–57164, dentaries with P_4–M_1; UWBM 57165, dentary with P_4–M_2; UWBM 57166–57169, dentaries with P_4; UWBM 57170–57171, dentaries with lower incisor; UWBM 57172–57173, M_1; from locality A8803, Ordnance.

UWBM 57175, 69 upper incisors, 28 lower incisors; UWBM 57176, rostrum with incisor; UWBM 57177–57178, maxillaries with P^4–M^2; UWBM 57179–57180, maxillaries with P^4–M^1; UWBM 57181 maxillary with broken P^4 and complete M^1–M^2; UWBM 57182–57184, 57186, maxillaries with P^4; UWBM 57185, maxillary with M^2–M^3; UWBM 57187, maxillary (edentulous); UWBM 57188, P^4; UWBM 57189, dentary with P_4–M_1; UWBM 57206, dentary with M_1–M_2; UWBM 57207, dentary with M_2; UWBM 57208–57210, dentaries (edentulous); UWBM 57211–57212, M_1; from the buff siltstones and sandstones at locality C0127, Arlington 14.

UWBM 57214, 2 upper incisors, 1 lower incisor; UWBM 57213, 3 upper incisors, 3 lower incisors; UWBM 57217, maxillary with P^4; UWBM 57218, dentary with lower incisor, P_4; UWBM 57219–57220, dentaries with lower incisor; UWBM 57221, M_1; from the buff siltstones and sandstones at locality C0120, Arlington 7.

UWBM 57222, 8 upper incisors, 6 lower incisors; UWBM 57223, dentary with M_1–M_3; from locality C0126, Arlington 13.

UWBM 57224, 3 upper incisors, 2 lower incisors from the conglomerate layer at locality B1533, Arlington 4.

UWBM 57225, lower incisor from the conglomerate layer at locality C0125, Arlington 12.

UWBM 57226, upper incisor, 2 lower incisors from the buff siltstones and sandstones; UWBM 57227–57228, lower incisors from the top of the buff siltstones and sandstones; locality B1532, Arlington 3.

UWBM 57229–57232, lower incisor, upper incisor from buff siltstones and sandstones; UWBM 57233, 5 upper incisors, 3 lower incisors; UWBM 57234, maxillary with M^1–M^2; UWBM 57235, dentary with P_4; from the base of the red siltstones; locality C0124, Arlington 11.

UWBM 57236, dentary with incisor; UWBM 57237, 2 upper incisors; from the base of the red siltstone from locality C0122, Arlington 9.

Table 1.—*Significance of difference of the anteroposterior length of P_4 in Tertiary species of* Perognathus.

Variate	Interval	Probability	Species[1]
P_4 AP	(0.0–0.8)(0.8–1.05)	.028	n:f
P_4 AP	(0.0–0.9)(0.9–1.35)	>.001	n:s
P_4 AP	(0.0–0.7)(0.7–0.9)	.30	mi:n
P_4 AP	(0.0–0.7)(0.7–0.9)	.109	d:n
P_4 AP	(0.0–0.7)(0.7–0.9)	.655	n:ma
P_4 AP	(0.0–0.8)(0.8–0.9)	.382	h:n
P_4 AP	(0.0–0.9)(0.9–1.05)	.014	n:r
P_4 AP	(0.0–0.75)(0.75–0.9)	>.001	p:n
P_4 AP	(0.0–0.9)(0.9–1.0)	.438	g:n
P_4 AP	(0.0–0.75)(0.75–0.9)	.509	ml:n
P_4 AP	(0.0–0.75)(0.75–0.9)	.011	pa:n

[1] Abbreviations and localities: d—*P. dunklei* (sec. 25, T105, R38W), f—*P. furlongi* (UCMP J-5847, V-863, V-6604), g—*P. gidleyi* (sec. 22, T335, R29W), h—*P. henryredfieldi* (UALP 29), ma—*P. mclaughlini* (sec. 36, T34S, R31W), mi—*P. minutus* (UCMP U-5847), ml—*P. maldei* (sec. 32, T7S, R13E), n—*Perognathus stevei*, p—*P. pearlettensis* (sec. 35, T34S, R30W), pa—*P. parvus*, r—*P. rexroadensis* (sec. 35, T34S, R30W), s—*P. saskatchewanensis* (sec. 31, T2N, R30W); mc—specimens from McKay Reservoir.

Table 2.—*Significance of difference of the transverse width of P_4 in Tertiary species of* Perognathus.

Variate	Interval	Probability	Species[1]
P_4 T	(0.0–0.8)(0.8–1.05)	.063	n:f
P_4 T	(0.0–0.9)(0.9–1.3)	>.001	n:s
P_4 T	(0.0–0.7)(0.7–0.9)	.10	mi:n
P_4 T	(0.0–0.8)(0.8–0.9)	.382	d:n
P_4 T	(0.0–0.8)(0.8–0.9)	.382	ma:n
P_4 T	(0.0–0.8)(0.8–0.9)	.255	h:n
P_4 T	(0.0–0.9)(0.9–1.05)	.001	n:r
P_4 T	(0.0–0.8)(0.8–0.9)	.014	p:n
P_4 T	(0.0–0.9)(0.9–0.95)	.175	n:g
P_4 T	(0.0–0.85)(0.85–0.9)	.109	n:ml
P_4 T	(0.0–0.9)(0.9–1.0)	.175	n:pa

[1] For abbreviations see Table 1.

UWBM 57238–57239, upper incisor, lower incisor from the top of the buff siltstones and sandstones; UWBM 57240, upper incisor from base of the red siltstones; locality B1534, Arlington 5.

UWBM 57241, 14 upper incisors, 11 lower incisors from locality C0141, Arlington 15.

Diagnosis.—A small form of *Perognathus* with: dentition hypsodont and lophodont; cingula on upper molars gently curving from paracone to protostyle, forming elongate fossettes; abbreviated anterior profile on P^4; lophs connecting lingually on M^2 and usually M^1; lophs connecting medially at early stage of wear on lower cheek teeth, P^4, and sometimes M^1. Normally bilaterally symmetrical P_4 with anteroconid; no accessory medial cuspules or ridges on P_4; posterior lophid frequently elongated by addition of hypostylid on P_4; anterior root of M_1 composed of two closely appressed columns.

Etymology.—Named for W. Steve Nelson in recognition of his invaluable assistance in the field.

Description.—In size and general morphology, these specimens resemble those of the extant species, *Perognathus parvus,* which now inhabits the region, the Hemphillian species, *P. henryredfieldi* Jacobs (1977) from Arizona and *P. dunklei* Hibbard (1939) from Kansas, and the Blancan species, *P. mclaughlini* Hibbard (1949) from Kansas and Arizona (Jacobs, 1977), *P. gidleyi* Hibbard (1941*a*) from Kansas, and *P. maldei* Zakrzewski (1969) from Idaho (Figs. 2–5, Tables 1–3). In *P. stevei* the transverse width of P_4 is shorter than that of *P. maldei* (Fig. 3, Table 2), which has a prominent hypostylid on the hypolophid. *P. stevei* is significantly smaller than the Blancan species, *P. rexroadensis* Hibbard (1950) from Kansas, and the Barstovian species, *P. saskatchewanensis* Storer (1970) and *P. furlongi* Gazin (1930) from California; but larger than the Clarendonian species, *P. minutus* James (1963) from California and *P. trojectioansrum* Korth (1979) from Nebraska and the Blancan species *P. pearlettensis* Hibbard (1941*b*) from Kansas. It should be noted that there is greater intraspecific variation of the size and structure of P_4 than of M_1.

Besides size, distinctive characteristics of individual teeth and differences in hypsodonty tend to separate specimens of *P. stevei* from those of other described species. All species described from Barstovian and Clarendonian deposits have much more

Table 3.—*Significance of difference of the anteroposterior and transverse dimensions of M_1 in Tertiary species of* Perognathus.

Variate	Interval	Probability	Species[1]
M_1 AP	(0.0–1.1)(1.1–1.2)	.083	n:f
M_1 AP	(0.0–0.8)(0.8–1.1)	.083	mi:n
M_1 AP	(0.0–1.05)(1.05–1.1)	.333	n:d
M_1 AP	(0.0–0.9)(0.9–1.1)	.167	n:ma
M_1 AP	(0.0–1.1)(1.1–1.3)	.009	n:r
M_1 AP	(0.0–1.0)(1.0–1.1)	.017	p:n
M_1 AP	(0.0–1.0)(1.0–1.15)	.181	n:g
M_1 AP	(0.0–1.1)(1.1–1.15)	.154	n:ml
M_1 AP	(0.0–0.9)(0.9–1.1)	.550	n:pa
M_1 T	(0.0–1.25)(1.25–1.35)	.083	n:f
M_1 T	(0.0–1.0)(1.0–1.25)	.083	mi:n
M_1 T	(0.0–0.95)(0.95–1.25)	.083	d:n
M_1 T	(0.0–1.15)(1.15–1.25)	.667	n:ma
M_1 T	(0.0–1.25)(1.25–1.4)	>.001	n:r
M_1 T	(0.0–1.15)(1.15–1.25)	.139	p:n
M_1 T	(0.0–1.1)(1.1–1.3)	.242	n:g
M_1 T	(0.0–1.2)(1.2–1.25)	.299	n:ml
M_1 T	(0.0–1.25)(1.25–1.3)	.450	n:pa

[1] For abbreviations see Table 1.

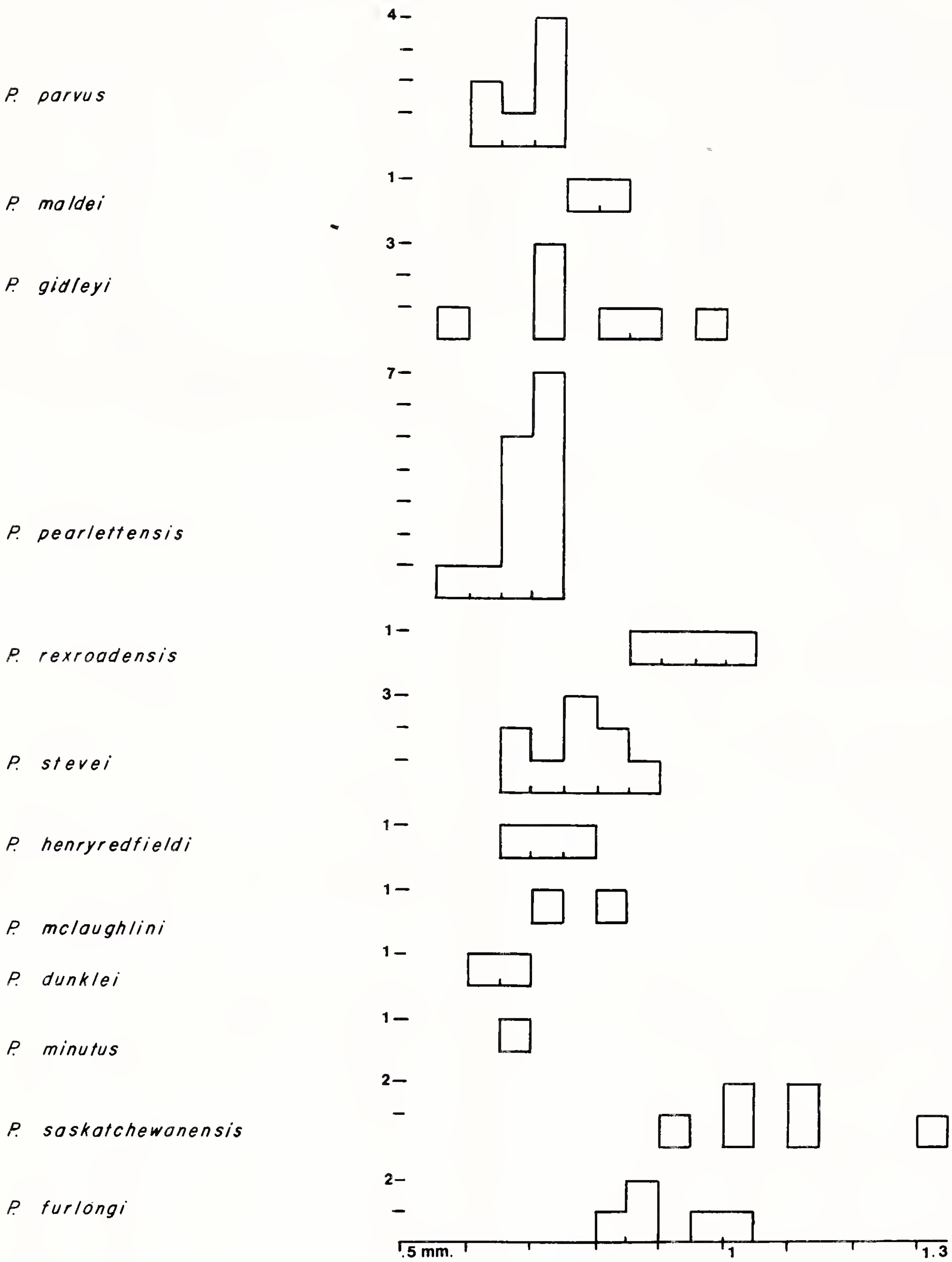

Fig. 2.—Distribution of the anteroposterior length of P_4 in Tertiary species of *Perognathus*. (Specimens designated as *P. stevei* represent all the very small geomyoid material from the Ordnance and Arlington localities.)

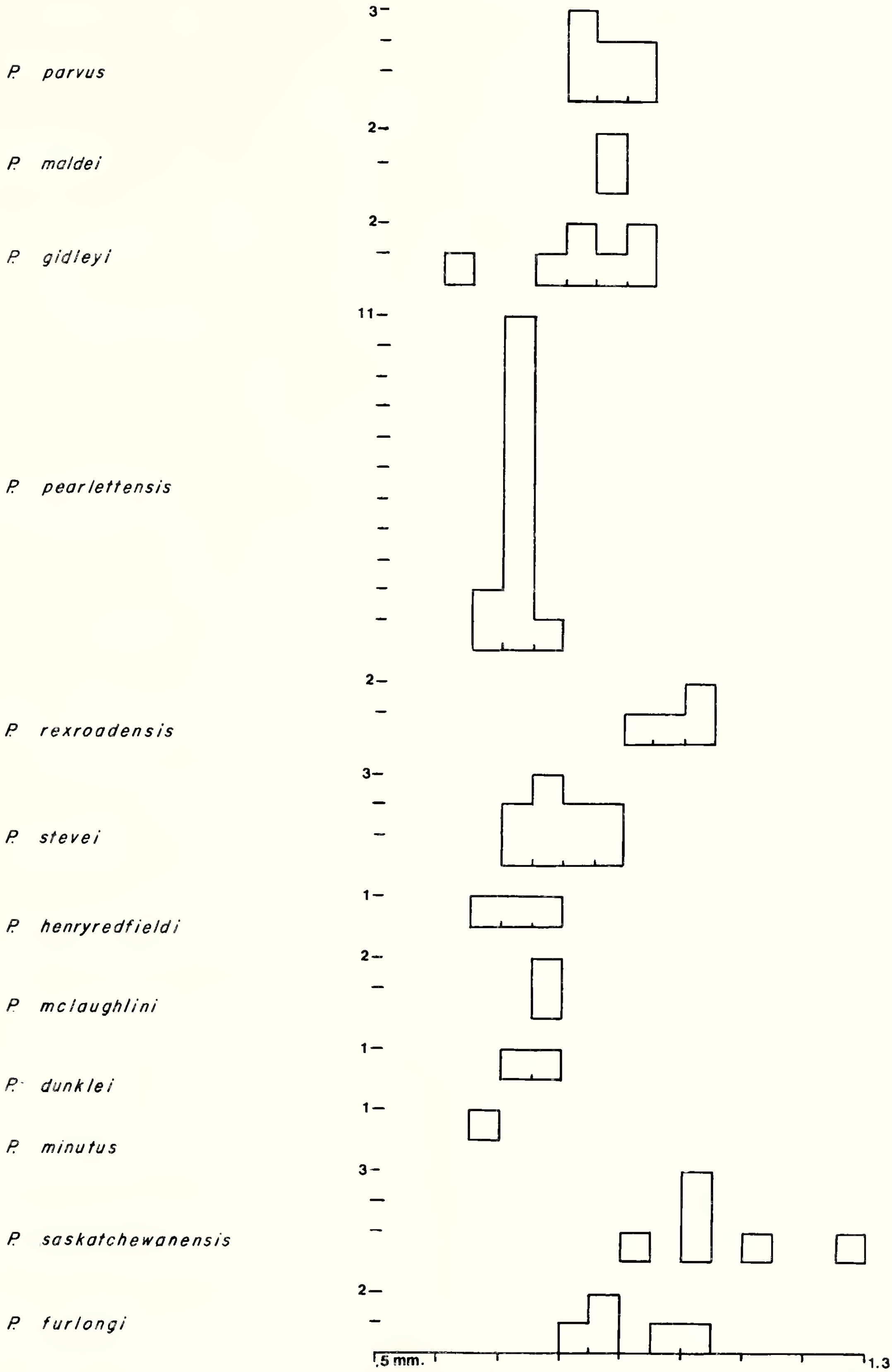

Fig. 3.—Distribution of the transverse width of P_4 in Tertiary species of *Perognathus*. (See Table 1 for localities of species.)

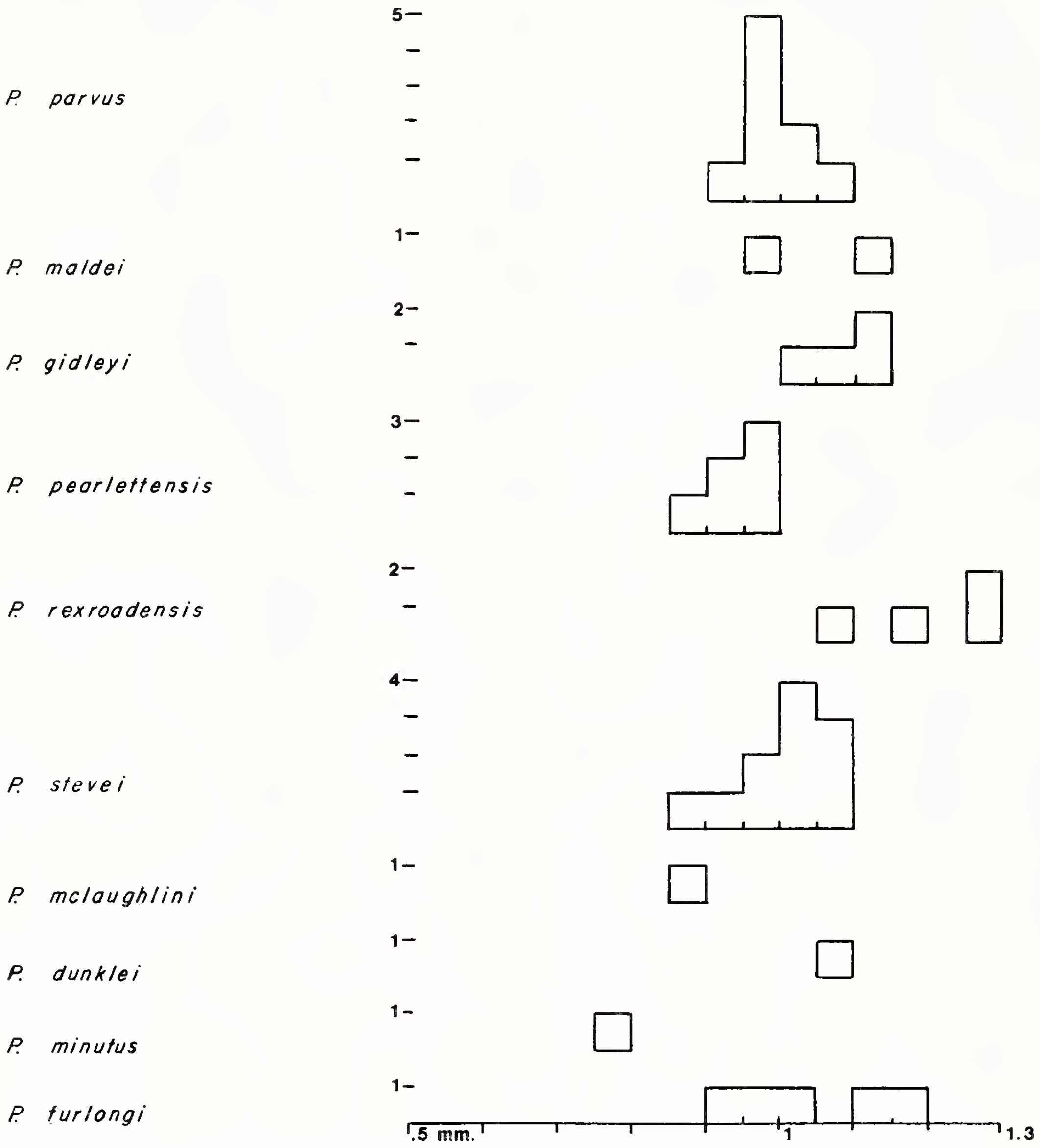

Fig. 4.—Distribution of the anteroposterior length of M_1 in Tertiary species of *Perognathus*. (See Table 1 for localities of species.)

brachyodont dentitions than *P. stevei*, and only in the teeth of *P. pearlettensis*, *P. rexroadensis*, *P. gidleyi*, *P. dunklei*, *P. maldei*, and *P. parvus* are the crown heights similar. Measurements of the lophs on little-worn teeth of these species can be compared (Figs. 6–7, Table 4); however, unworn teeth are not known for some species. For example, *P. dunklei* from the Edson Quarry in Kansas was considered by Hibbard (1939:458) to have a hypsodont dentition, but the type specimen possesses very worn teeth. From Hibbard's figure (p. 462), it appears that only traces of the reentrants of the P_4 remain, whereas the lophids of M_1 are not joined, and those of M_2 have just merged. UWBM 57165 (Fig. 8) is a dentary with worn teeth on which the lophids of the M_2 have been joined medially for some time so even a buccal connection has formed, and the lophids of M_1 have also met and joined. This indicates that the individual is ontogenetically older than the type specimen of *P. dunklei*. However, the P_4 of UWBM 57165 retains deep reentrants indicating a more hypsodont tooth. In addition, an anterior bulge is present in the position of the anteroconid. No anteroconid exists on the type or referred specimen of *P. dunklei*.

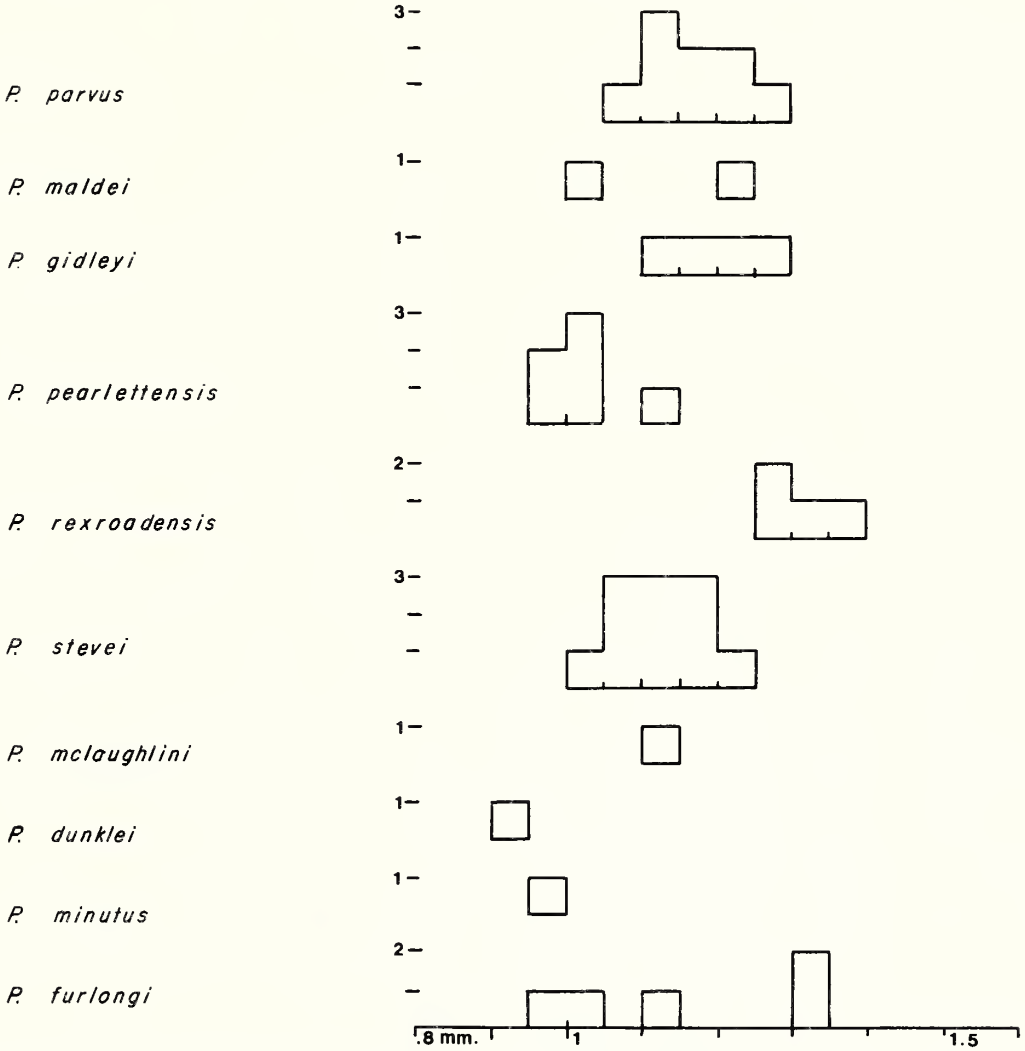

Fig. 5.—Distribution of the transverse width of M_1 in Tertiary species of *Perognathus*. (See Table 1 for localities of species.)

P. maldei from the Hagerman fauna is likewise known from only a few specimens with worn dentitions. The type specimen, UMMP 55183, is the least worn, but enough so that a reliable measurement of hypsodonty could not be made. Visual comparison of this specimen with those of *P. stevei* at about the same stage of wear indicates that *P. maldei* has an equal or greater degree of hypsodonty than *P. stevei*. Figs. 6–7 and Table 4 illustrate the differences in the specimens whose hypsodonty could be measured. Frequency distributions for the height of the posterior lophid of P_4 and for the anterior lophid of M_1 measured from the base of the lingual valley to the tip of the lophid were plotted, as well as the ratio of the lophid height to the anteroposterior dimension. Although there is range overlap, these differences indicate that *P. pearlettensis, P. gidleyi,* and *P. rexroadensis* have lower-crowned teeth than *P. stevei,* and that *P. parvus* is more hypsodont than the latter species.

The deeply grooved, highly curved incisor of *P. stevei* is identical to that of the Recent pocket mice. Of species in which the anterior root of the zygomatic process is preserved, those of *P. stevei, P. rexroadensis,* and *P. pearlettensis* flare laterally, whereas those of *P. parvus, P. gidleyi,* and *P. furlongi* are directed dorsoventrally, forming a deep infraorbital fossa similar to that of the geomyines.

The upper premolars of species of the Perognathinae are similarly constructed, normally with a

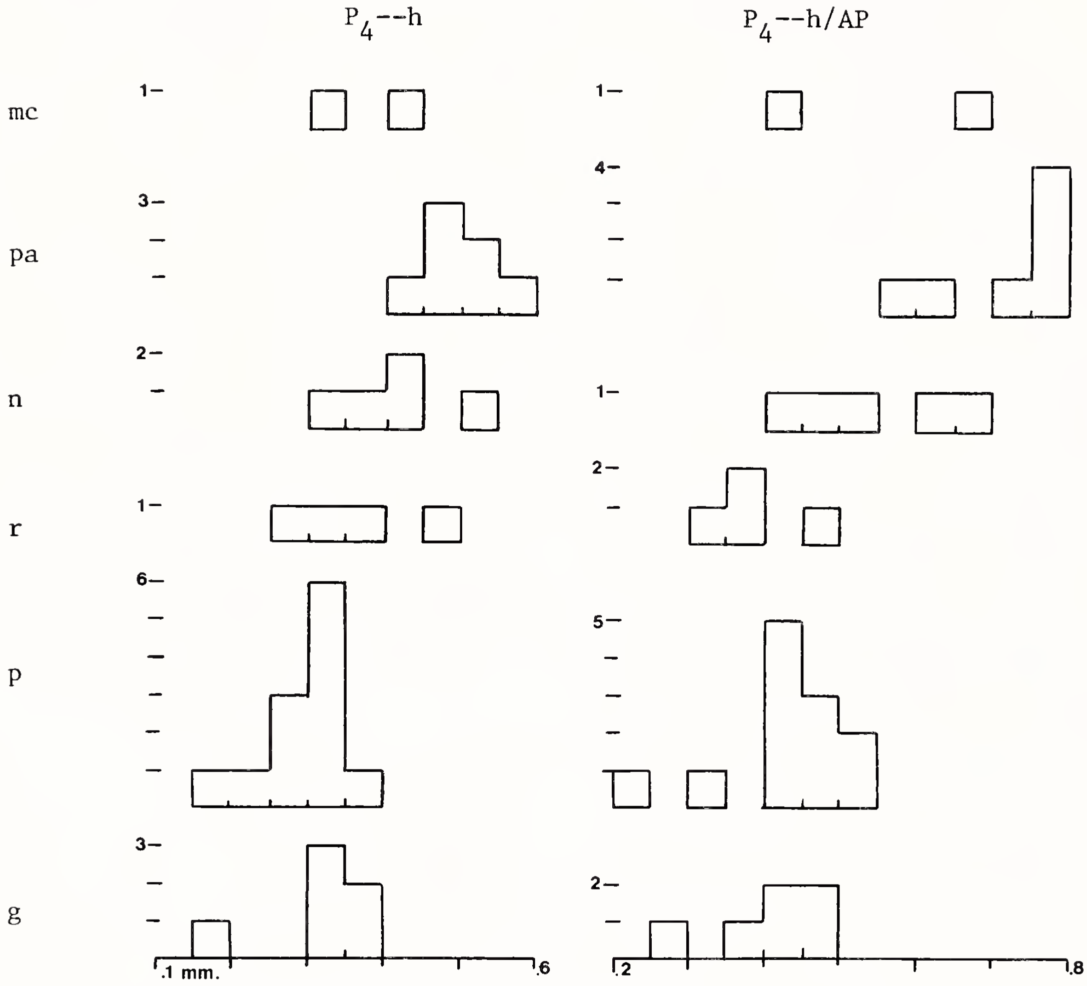

Fig. 6.—Distribution of the height (h) of the posterior lophid of P_4 and of the ratio of the height to the anteroposterior length in Tertiary species of *Perognathus*. (See Table 1 for abbreviations of species.)

single cusped protoloph and a tricusped metaloph, but some differences exist. In *P. furlongi* the crowns are very bulbous and in some specimens of P^4, a small accessary cuspule is present on the protoloph buccal to the protocone, whereas the cheek teeth of *P. stevei* are not inflated and the protoloph of the P^4 is always a single cusp beneath which the root is directed downward, forming an abbreviated anterior profile. On *P. furlongi* and *P. parvus* the protocone is slanted anteriorly so its root projects far forward, forming a continuous slope along the anterior profile. Also in UCMP 49364, a P^4 of *P. furlongi*, the lophs are connected buccally, a feature unknown on the P^4 of *P. stevei*. Some specimens of *P. parvus* exhibit the abbreviated profile, but on no specimens of *P. stevei* is the slope profile constant. The occlusal pattern of the metaloph of *P. stevei* is a gently curved transverse ridge, unlike that of *P. parvus*, which is angulate due to the anterior position of the metacone and hypostyle. The hypostyle is sometimes anteriorly located, depending on the development of the posterior cingulum, which ranges from absence, in only UWBM 57155, to a more commonly occurring crest extending between the posterior margins of the hypostyle and hypocone, as in UWBM 57154.

Configuration of the M^1 and M^2 is similar to the condition in *P. parvus*, but some differences are apparent: (1) the teeth of *P. stevei* are less hypsodont, are shorter transversely (Table 5), and are more robust. A shallow valley which widens internally divides the lophs, and with wear the molars do not retain a cuspate pattern as long as do those of other fossil species. (2) The loph connection on M^1 is nor-

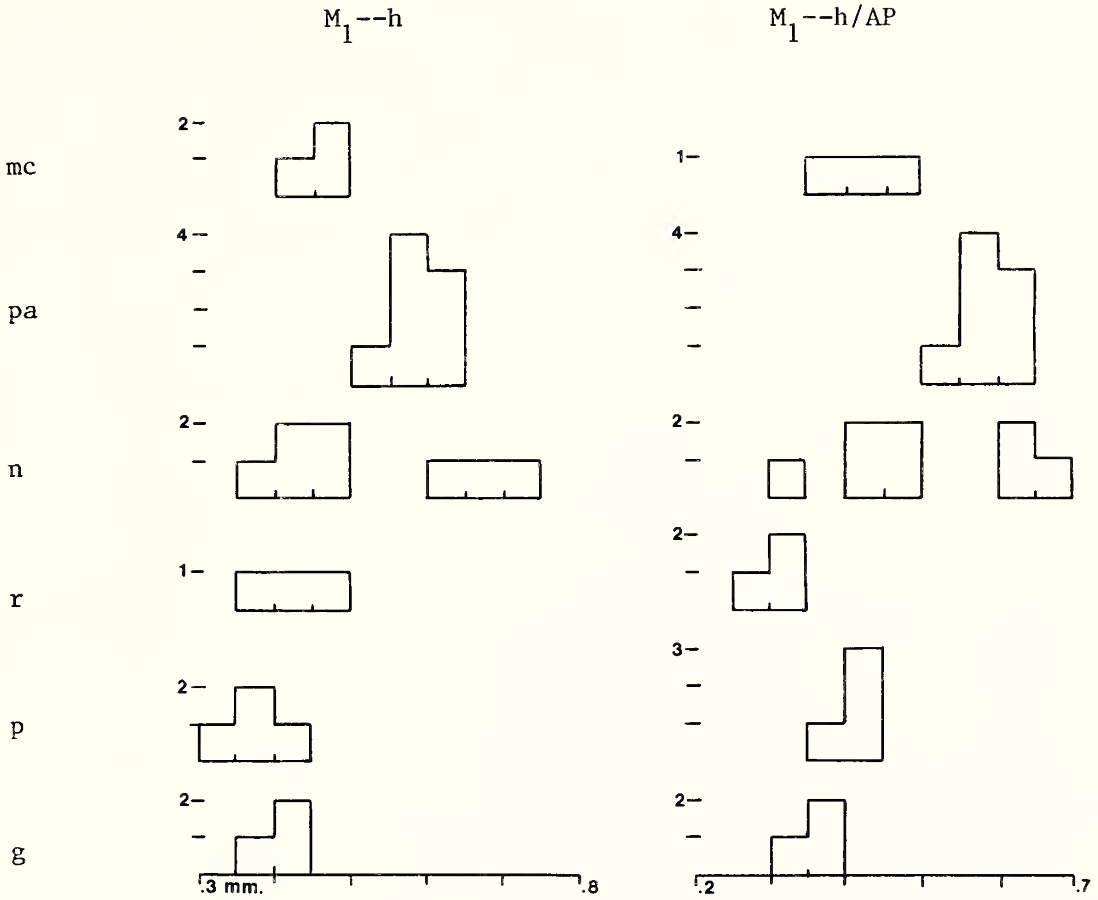

Fig. 7.—Distribution of the height (h) of the anterior lophid of M_1 and of the ratio of the height to the anteroposterior length in Tertiary species of *Perognathus*. (See Table 1 for abbreviations of species.)

mally lingual, but can occur medially and lingually at about the same time, whereas union always occurs medially on the M^1 of *P. parvus.* (3) Loph union on M^2 is always lingual in *P. stevei* but is medial on many specimens of *P. parvus.* On UWBM 57234, the lophs of M^1 connect medially, but those of M^2 connect lingually. (4) The anterior cingulum of the M^1 normally forms an arc, which originates from the paracone, extends around the anterior face of the protocone, and merges with the protostyle, forming a long, transverse fossette with greater wear. This cingulum on the extant species flares anteriorly from the paracone, abruptly turns laterally, and reaches only to the protocone. On some specimens of *P. stevei* (For example UWBM 57153, Fig. 9, a) an angular bend is formed, but the crest still reaches to the protostyle, and a few specimens have a short crest extending only to the protocone. No anterior cingula exist on the molars of KU 7740, a paratype

Table 4.—*Significance of difference of the hypsodonty in some species of* Perognathus.

Variate	Interval	Probability	Species[1]
P_4 h[2]	(0.0–.40)(.40–.55)	.061	g:n
P_4 h	(0.0–.40)(.40–.55)	.015	p:n
P_4 h	(0.0–.50)(.50–.55)	.556	r:n
P_4 h	(0.0–.40)(.40–.60)	.152	pa:n
P_4 h/AP	(0.0–.50)(.50–.70)	.061	g:n
P_4 h/AP	(0.0–.55)(.55–.70)	.074	p:n
P_4 h/AP	(0.0–.50)(.50–.70)	.119	r:n
P_4 h/AP	(0.0–.55)(.55–.80)	.046	pa:n
M_1 h[3]	(0.0–.45)(.45–.75)	.121	g:n
M_1 h	(0.0–.45)(.45–.75)	.071	p:n
M_1 h	(0.0–.50)(.50–.75)	.339	r:n
M_1 h	(0.0–.50)(.50–.75)	.013	n:pa
M_1 h/AP	(0.0–.40)(.40–.70)	.024	g:n
M_1 h/AP	(0.0–.45)(.45–.70)	.071	p:n
M_1 h/AP	(0.0–.35)(.35–.70)	.024	r:n
M_1 h/AP	(0.0–.50)(.50–.70)	.013	n:pa

[1] For abbreviations of species see Table 1.
[2] Height of the posterior lophid of P_4 measured from the base of the lingual valley.
[3] Height of the anterior lophid of M_1 measured from the base of the lingual valley.

Table 5.—*Measurements of* Perognathus stevei.

Tooth	N	Observed range	Mean	S	CV
Locality A8803, Ordnance					
P^4-AP	8	.65–.85	.74 ± .06	.07 (.05–.14)	9.8 ± 4.8
P^4-T	8	.80–1.15	.98 ± .12	.14 (.09–.28)	14.28 ± 7.0
M^1-AP	5	.82–.94	.89 ± .06	.05 (.03–.14)	5.62 ± 3.48
M^1-T	5	1.16–1.25	1.21 ± .05	.04 (.02–.15)	3.31 ± 2.05
M^2-AP	4	.73–.80	.78 ± .05	.03 (.02–.11)	3.85 ± 2.67
M^2-T	4	1.05–1.14	1.08 ± .08	.05 (.03–.19)	4.63 ± 3.21
P_4-AP	7	.65–.85	.77 ± .07	.07 (.05–.15)	9.09 ± 4.76
P_4-T	7	.76–.88	.81 ± .06	.06 (.04–.13)	7.41 ± 3.88
M_1-AP	5	.90–1.08	1.0 ± .08	.06 (.04–.17)	6.0 ± 3.72
M_1-T	5	1.06–1.21	1.12 ± .08	.06 (.04–.17)	5.36 ± 3.32
Locality C0127, Arlington 14					
P^4-AP	8	.70–.85	.79 ± .05	.06 (.04–.12)	7.54 ± 3.7
P^4-T	9	.90–1.24	1.12 ± .11	.14 (.10–.27)	12.5 ± 5.77
M^1-AP	6	.89–.95	.93 ± .03	.03 (.02–.07)	3.23 ± 1.83
M^1-T	6	1.21–1.28	1.25 ± .03	.03 (.02–.07)	2.40 ± 1.36
M^2-AP	4	.73–.84	.76 ± .08	.05 (.03–.19)	6.58 ± 4.56
M^2-T	4	.89–1.12	1.06 ± .11	.07 (.04–.26)	6.6 ± 4.57
M^3-AP	1		.75		
M^3-T	1		.87		
P_4-AP	1		.75		
P_4-T	1		.79		
M_1-AP	4	.87–1.08	.99 ± .14	.09 (.05–.34)	9.09 ± 6.3
M_1-T	4	1.01–1.17	1.09 ± .11	.07 (.04–.26)	6.42 ± 2.27
M_2-AP	2	.75–.96	.86		
M_2-T	2	.92–1.15	1.04		

Museum no.	Specimen	AP	T
Locality C0120, Arlington 7			
UWBM 57217,	maxillary P^4	.75	.87
UWBM 57218,	dentary P_4	.68	.70
UWBM 57221,	M_1	1.05	1.17
Locality C0126, Arlington 13			
UWBM 57223,	dentary M_1	.96	1.19
	M_2	.93	1.18
	M_3	.80	.86
Locality C0124, Arlington 11			
UBWM 57234,	maxillary M^1	.90	1.25
	M^2	.75	1.05

of *P. mclaughlini* (Hibbard, 1949, fig. 2), and those of *P. rexroadensis* are poorly formed, consisting of an anterior spur from the paracone.

From Arlington 14 a moderately worn specimen of M^3 was collected which does not seem to be as small or as delicate as that of *P. parvus.* Also, the anterior cingulum of this tooth, UWBM 57185 (Fig. 9, c), is continuous between the paracone and the protostyle. On *P. parvus* a shorter crest terminates at the protocone, and on *P. rexroadensis* only the anterior spur is present.

The lower incisor is smooth-faced, long, and gently curved, and the dentary fragments are identical to those of *P. parvus.* No ascending rami were recovered, but the dentaries have a prominent, dorsally rising masseteric crest, and the mental foramen is situated below the diastema. UWBM 57189 (Fig. 10, a) from Arlington 14 has a slightly more robust dentary with a heavier, wider diastema than that of the other specimens of *P. stevei.* However, the dentition is of the same size and structure as that of other specimens of *P. stevei* from the same locality, indicating that the robust dentary of UWBM 57189 represents intraspecific variation.

The alveoli in the mandibles indicate the presence of two wide roots on M_1, but on isolated molars the anterior root can be seen to be composed of two closely appressed columns. This condition differs from that of *P. parvus* and *P. maldei,* which have well divided anterior roots. On no other fossil species could the appressed columns, representing incipient division, be observed. Also, the alveoli for the posterior root of M_1 and the anterior root of M_2 of *P. stevei* are confluent.

Although the P_4 of *P. stevei* retains the characteristic quadrate pattern of *Perognathus* with medial union of the cusps, the tooth exhibits some variability as does that of the Recent species. Five of eight premolars have a distinct anteroconid which lies between the protoconid and metaconid, not at the end of a medial ridge like that of *P. saskatchewanensis* (Storer, 1975: 93) from the Wood Mountain Formation. Anteroconids are unknown on the lower premolars of *P. henryredfieldi, P. mclaughlini, P. rexroadensis, P. dunklei,* and *P. maldei.* Of described species, *P. minutus, P. gidleyi,* and *P. pearlettensis* possess the cuspule, and as in *P. stevei,* the presence of the cuspule is variable. Only one specimen of *P. minutus,* UCMP 76987, has the cuspule.

The manner of lophid union on the P_4 of *P. stevei* is quite variable. On UWBM 57166 and 57189 (Fig. 10, a) union occurs between the metaconid and entoconid. Four premolars have a connection between the protoconid and hypoconid, and UWBM 57167 has a double connection: a crest extends from each anterior cusp to the cusp directly posterior. No specimens of *P. stevei* have medial cuspules or ridges, such as the well defined ridge of *P. saskatchewanensis. P. mclaughlini* and *P. pearlettensis* always have prominent lophid connections between the protoconid and hypoconid.

Except for the closely appressed metaconid and protoconid of UWBM 57189, these cusps are well divided on the other premolars of *P. stevei,* and the reentrants are of about equal depth and cross the same occlusal distance, resulting in a symmetrical tooth. Due to the protoconid-hypoconid connection of the P_4 of *P. mclaughlini, P. henryredfieldi, P. rexroadensis,* and *P. pearlettensis,* their reentrants are asymmetrical. In *P. pearlettensis* and *P. mclaughlini* the lingual valleys are very wide and deep, and the P_4 of the latter species is very bulbous compared with that of *P. stevei.* The protoconid is larger than the metaconid on *P. rexroadensis,* accentuating the asymmetry of the tooth. In *P. saskatchewanensis* a transversely compressed metalophid and widely separated lophids result in a rectangular outline, whereas in *P. stevei* the metalophid and hypolophid are of about the same transverse dimension and are close enough to form a quadrate outline.

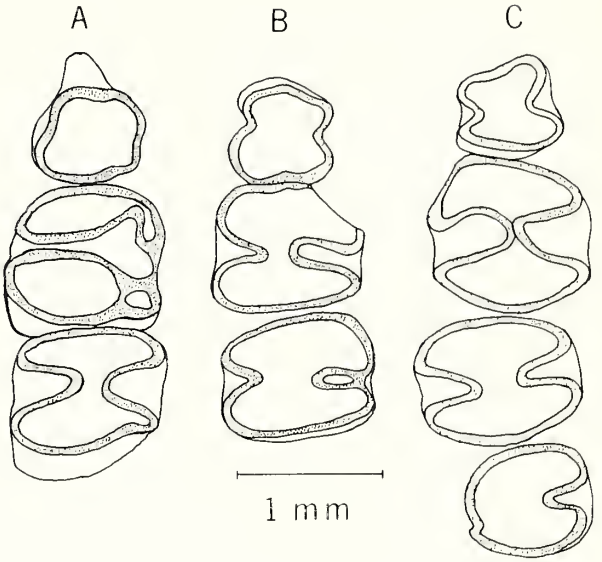

Fig. 8.—Wear patterns on some species of *Perognathus.* A) *Perognathus dunklei,* MCZ 6203, right P_4–M_2 (illustration modified from Hibbard, 1939); B) *P. stevei,* UWBM 57165, right P_4–M_2; C) *P.* species indeterminate, UWBM 57902, left P_4–M_3.

Construction of the hypolophid also varies. Besides the hypoconid and entoconid, which with wear unite first, two premolars, UWBM 57166 and 57189, have a small buccal cusp on the hypolophid which is similar to, but not as large as, the hypostylid of *P. maldei* and *P. parvus.* On some specimens of *P. rexroadensis* and *P. gidleyi,* a small cuspule appears between the hypoconid and entoconid, resulting in a longer hypolophid, perhaps paralleling that of *P. maldei* and some specimens of *P. stevei.* The hypolophid of *P. stevei* is extremely lophate and forms a transverse crest with wear. There is no deep posterior indentation of the hypolophid as is the case with the paratype of *P. dunklei,* which exhibits the X-pattern to an extreme degree.

The roots of the P_4 of *P. stevei* are widely divided, whereas those of *P. henryredfieldi* are fused proximally.

The lower molars are lower-crowned than those of *P. parvus,* and the construction of the anterobuccal cingulid differs. On the Recent species the anterior margin of the metalophid is pointed because the cingulid originates from a posteriorly positioned protostylid and extends anterior to and isolates the protoconid, where it bends posteriorly and connects

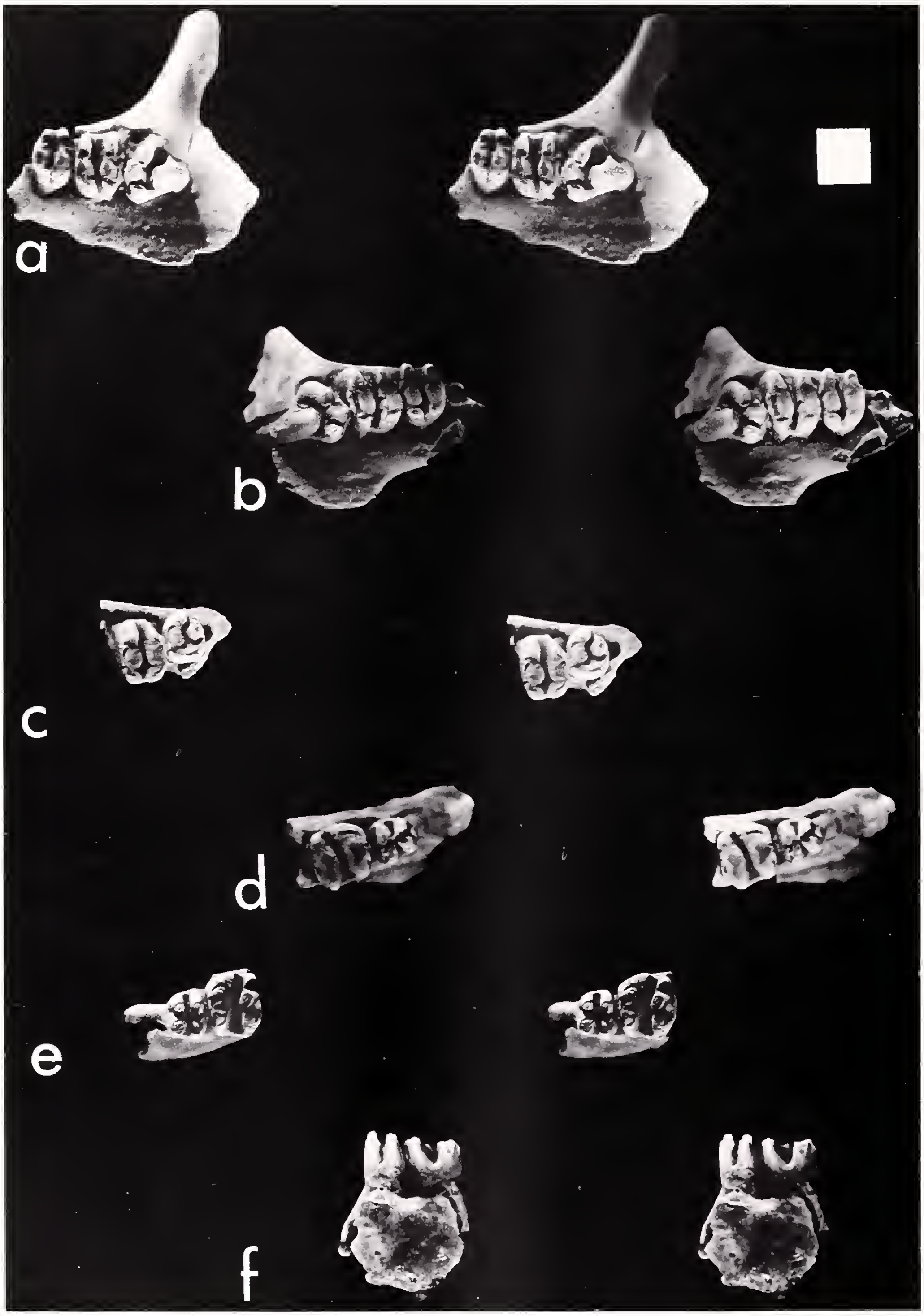

Fig. 9.—Selected specimens of *Perognathus stevei.* a) UWBM 57153, right maxillary with P^4–M^2 (holotype); b) UWBM 57152, left maxillary with P^4–M^2; c) UWBM 57185, left maxillary with M^2–M^3; d) UWBM 57163, left dentary with P_4–M_1; e) UWBM 57164, right dentary with P_4–M_1; f) UWBM 57164, right dentary with P_4–M_1, lingual view. Scale equals one millimeter.

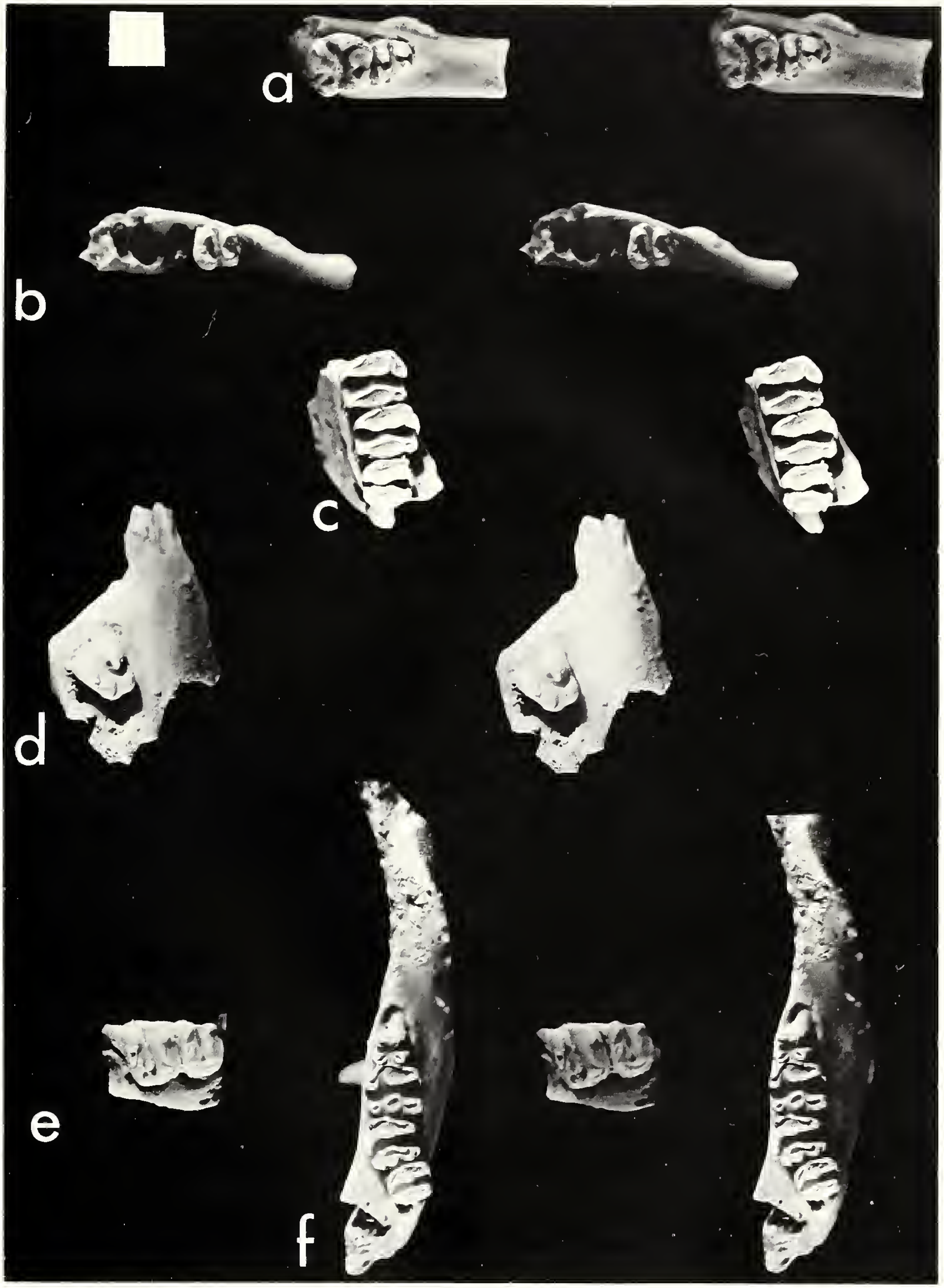

Fig. 10.—Selected specimens of *Perognathus stevei* and *P.* species indeterminate. a) *P. stevei,* UWBM 57189, left dentary with P_4–M_1; b) *P. stevei,* UWBM 57176, left dentary with P_4; c) *P. stevei,* UWBM 57223, right dentary with M_1–M_3; d) *P.* species indeterminate, UWBM 57974, right maxillary with P^4; e) *P.* species indeterminate, UWBM 57974, left maxillary with M^1–M^2; f) *P.* species indeterminate, UWBM 57974, left dentary with P_4–M_3. Scale equals one millimeter.

between the protoconid and metaconid. On *P. stevei* and *P. maldei* the angular portion of the cingulid is anterobuccal to the protoconid, and the cingulid terminates at the buccal side of the protoconid. On *P. minutus* the anterior cingulid is not angular, but rounded. Also, the protoconids of the molars of *P. stevei* are never as isolated internally as those of *P. parvus.* Lophid union first occurs medially on molars of *P. stevei,* but a buccal connection can soon form on some specimens. The hypolophid is high, and the hypostylid of *P. stevei* is a prominent cusp which is almost as high as the hypoconid and entoconid. On all other fossil species, except *P. pearlettensis* and *P. maldei,* the hypostylid is low.

Discussion

P. stevei is more hypsodont than other species of *Perognathus* from Hemphillian and older deposits. Only *P. maldei* from the Blancan Hagerman fauna and the Recent pocket mouse, *P. parvus,* are higher-crowned. *P. stevei* can be distinguished from these species on the basis of smaller size, particularly of the P_4, presence of anteroconids, poorly formed hypostylids when present on P_4, and incipient division of the anterior root of M_1. None of these differences precludes *P. stevei* from the ancestry of the Recent species through a form such as *P. maldei.*

***Perognathus* species indeterminate**

Referred specimens.—UWBM 57783, 5 upper incisors; UWBM 57973, 2 upper incisors; UWBM 57974, upper incisor, maxillary with P^4, isolated M^1, maxillary with M^1–M^2, dentary with P_4–M_3; UWBM 57905, M^2; UWBM 57979, dentary with P_4–M_1; UWBM 57902, dentary with P_4–M_3; UWBM 57903, dentary with M_1–M_3; UWBM 57904, M_1; UWBM 57975, P_4; from locality C0128, McKay Reservoir.

This sample represents the total of small, brachyodont geomyoid specimens from the McKay Reservoir site.

Description.—All specimens, except for UWBM 57783, were found by W. Steve Nelson in a coprolite associated with *Oregonomys sargenti* (Shotwell). Recovery of three right lower first molars indicates that at least three individuals of *Perognathus* were preserved in the concentration of bone. Two individuals are young adults with only slightly worn dentitions, and the third, represented by two mandibles, UWBM 57979 and 57902, is from an old individual whose teeth are so worn that the lophids have been united.

The P^4 (Fig. 10, d) exhibits the cusp pattern characteristic of *Perognathus.* The abbreviated anterior slope of the protocone is similar to the condition observed on the specimens from Arlington and Ordnance, but the hypostyle of UWBM 57974 is more inflected, and the metacone and hypocone are appressed, more like the premolar of *P. parvus.* The P^4 from McKay Reservoir is housed in a maxillary fragment, which appears to have had a very broad interpalatal distance, but poor preservation of the maxillary prohibits precise evaluation.

The upper molars (Fig. 10, e) are similar to those from the other northern Oregon localities, but some structures are distinct. Most obvious is the shorter, angular cingulum, which is like that of *P. parvus.* The angular construction of the cingulum was found on one specimen from Ordnance, UWBM 57153, but its cingulum is long and extends from the paracone to the protostyle, not a short anteriorly directed spur like the cingula on the specimens from McKay Reservoir. Specimens of M^1 of *Perognathus* species indeterminate are rather long with wide, shallow valleys, which separate the lophs, whereas the perognathine molars from Ordnance and Arlington are more anteroposteriorly compressed and lophate. Lingual connections have already occurred on both specimens of M^2. At equivalent wear stages, a gap remains between the lophs of M^2 on *P. stevei.* Overall, the upper molars from McKay Reservoir are slightly more brachyodont than those from the other northern Oregon localities, and have a cingulum structure which is more similar to that of the Recent species.

The horizontal rami of the older specimens are more robust and are deeper below the diastema than those of *P. parvus,* but the mandibles of the younger individuals are identical.

The lower cheek teeth resemble those of *P. stevei* with only minor differences. The P_4 (Fig. 10, f) is composed of four cusps arranged in a quadritubercular pattern; no hypostylid or anteroconid were observed as they were on P_4 of *P. stevei.* The cusps unite medially to form an X-pattern considered characteristic of the Perognathinae by Wood (1935: 96), and the roots of the premolars appear well divided, unlike those of *P. henryredfieldi.* Comparison of Table 6 with Table 5 indicates that the premolars and molars from McKay Reservoir are about the same size as those of *P. stevei,* and Figs. 6 and 7 and Table 7 indicate that the degree of hypsodonty is similar. Only the greater anteroposterior length of M_1 on some specimens from McKay Reservoir appears to be a distinctive character.

Table 6.—*Measurements of* Perognathus *species indeterminate from McKay Reservoir, locality C0128.*

Museum no.	Specimen	AP	T
UWBM 57974, maxillary	P^4	.70	1.10
isolated	M^1	.92	1.15
maxillary	M^1	.94	1.07
	M^2	.75	1.10
dentary	P_4	.59	.70
	M_1	1.04	1.01
	M_2	.98	1.04
	M_3	.74	.83
UWBM 57979, dentary	P_4	.75	.76
	M_1	1.19	1.16
UWBM 57903, dentary	P_4	.73	.75
	M_1	1.17	1.16
	M_2	.99	1.19
	M_3	.84	.96
UWBM 57903, dentary	M_1	1.04	1.10
	M_2	.98	1.13
	M_3	.81	.93
UWBM 57975, isolated	P_4	.75	.71
UWBM 57904, isolated	M_1	1.01	1.01
UWBM 57905, isolated	M^2	.73	.99

Table 7.—*Significance of difference of hypsodonty in* Perognathus stevei *and specimens of* Perognathus *from McKay Reservoir.*

Variate[1]	Interval	Probability	Species[1]
P_4 h	(0.0–.45)(.45–.55)	.714	mc:n
P_4 h/AP	(0.0–.40)(.40–.70)	1.0	mc:n
M_1 h	(0.0–.50)(.50–.75)	.339	mc:n
M_1 h/AP	(0.0–.50)(.50–.70)	.339	mc:n

[1] For abbreviations see Figure 6 and Table 1.

Two specimens of M_3 were recovered, of which one, UWBM 57974, is unworn. The metalophid on these specimens is similar to those on the M_1–M_2, except that the anterior cingulid does not extend as far anteriorly. Therefore, the leading edge of this molar is flat, not angular. The hypolophid is a transverse crest, but the hypostylid is reduced, resulting in a shorter lophid compared with the metalophid. With wear, a medial union between lophids occurs, and, on UWBM 57902, this union has extended across the buccal half of M_3. A medial connection has formed on P_4 and M_2 of this specimen, and an incipient connection occurs on M_1. Therefore, UWBM 57902 is slightly more worn than the type of *P. dunklei* Hibbard. UWBM 57902 differs from *P. dunklei,* as does UWBM 57165 from Ordnance, in retaining the crown pattern of P_4 after lophid union on M_1 (Fig. 8).

Discussion

These specimens were found at McKay Reservoir associated with elements of *Oregonomys sargenti* in a small concentration. Preservation, their intimate association, and the rarity of these taxa at McKay Reservoir indicate a coprolitic accumulation. With the exception of a few specimens mentioned by Shotwell (1967) and isolated incisors, UWBM 57783, these are the only known specimens of *Perognathus* from the locality. *Oregonomys sargenti* also appears to be scarce; only a few other isolated specimens have been found.

Because the specimens of *Perognathus* from McKay Reservoir include cheek teeth that have widely separated, cuspate lophs, they are not conspecific with *P. stevei.* Other differences from *P. stevei* include: (1) a greater inflection of the hypostyle on P^4; (2) the cingula on the upper molars is shorter and usually more angulate; (3) the lingual connection of lophs on M^2 occurs earlier; and (4) the P_4 does not possess an anteroconid or hypostylid and retains a square outline. The two species, however, are probably closely related as indicated by their similar size and geographic proximity. However, features resembling those of the Recent species such as short, angular cingula and inflection of the hypostyle on P^4 perhaps indicate a younger geological age of these specimens than those of *P. stevei.*

Heteromyinae Alston, 1876

Oregonomys, new genus

Genotypic species.—*Oregonomys pebblespringsensis* new species.

Referred species.—*Diprionomys agrarius* Wood, 1935; *Perognathus sargenti* Shotwell, 1956; *Perognathus magnus* Zakrzewski, 1969.

Distribution of genus.—Quinn Canyon locality in Nebraska; Arlington, Ordnance, and McKay Reservoir localities in Oregon; Hagerman locality in Idaho.

Age.—Clarendonian, Hemphillian, and Blancan.

Generic definition.—Palate wide; auditory region inflated; upper incisors grooved; robust, bilophate cheek teeth, with size decreasing posteriorly; protoloph of P^4 with buccal cuspule; lophs of P^4 connecting medially or lingually; three roots on P^4; lophs of upper molars connecting lingually; mental fora-

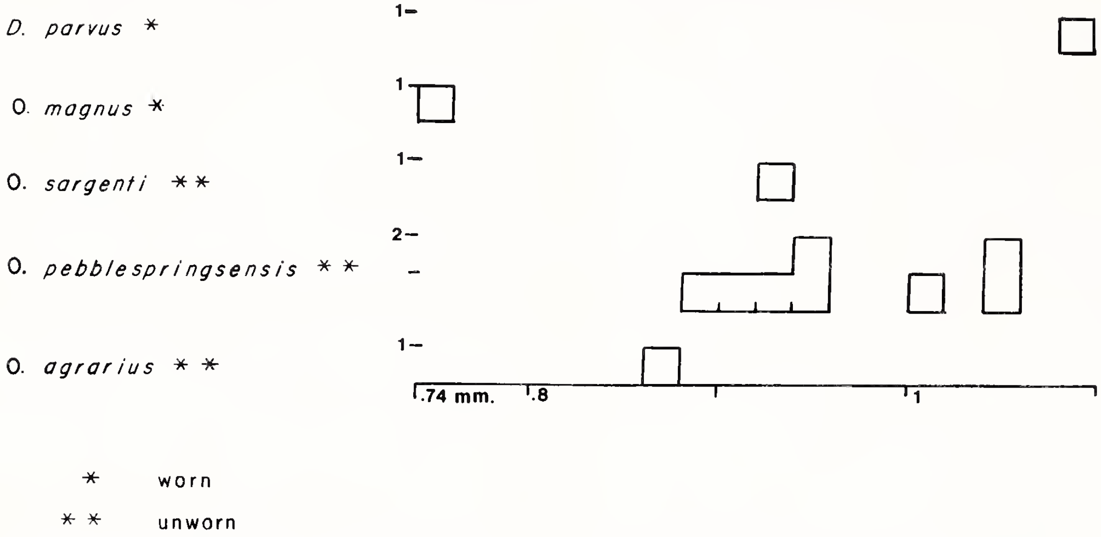

Fig. 11.—Distribution of the crown height of P_4 in the holotype of *Diprionomys parvus* and species of *Oregonomys*. (The material of *O. pebblespringsensis* represents all the larger brachyodont geomyoids from the Ordnance and Arlington localities.)

men below diastema, well anterior and below masseteric scar; coronoid process deflected; angular process expanded; tendency for molariform P_4; lophid connection of P_4 normally medial, sometimes buccal; lingual valley of P_4 not extending to base of tooth; connection of lophids on lower molars normally buccal, with tendency for medial union; postcranial skeleton adapted for ricochetal locomotion.

Etymology.—Named for the state in which the genotypic species was collected and from the Greek *mys* meaning mouse.

Discussion.—Although the previously described species, *O. sargenti* (Shotwell) and *O. magnus* (Zakrzewski) were referred to *Perognathus*, both authors expressed doubt about the assignment. Shotwell (1956:731), in particular, noted that the taxon was larger than Recent species of *Perognathus* and possessed six cusps on P_4 rather than four cusps arranged in a quadrate pattern. Zakrzewski (1969) appears to have followed the example of Shotwell (1956) and Wood (1935), who described the large species, *Perognathus coquorum* from the Upper Snake Creek beds in Nebraska. When Zakrzewski described *O. magnus* from the Hagerman fauna in Idaho, he had only a maxillary with slightly worn teeth and a dentary with very worn teeth. In 1978, Philip Bjork, from the South Dakota School of Mines and Technology, returned to the type locality of *O. magnus* and found a mandible containing slightly worn teeth. Through his kindness the description of this specimen, SDSM 8749, is included here. Our collections made from northern Oregon have produced about 60 maxillaries and dentaries with cheek teeth of a new species, *O. pebblespringsensis*, from Ordnance and Arlington and include additional specimens of *O. sargenti* from McKay Reservoir. The specimens of these three species of *Oregonomys* differ from those of *Perognathus* in larger size (almost a fourth larger than most extant species of *Perognathus*), possession of additional cuspules on the protoloph of P^4, often a buccal connection of lophs of P^4 at some wear stage, and a molariform P_4 which never forms an X-pattern.

Of other published genera, only *Diprionomys* has a similar morphology. *Diprionomys parvus* Kellogg (1910), the genotypic species from the Thousand Creek beds in Nevada, resembles *Oregonomys* in structure of P_4, but is more hypsodont, smaller, more delicately constructed, and the internal valley persists to the base of P_4. Of these characteristics, hypsodonty and persistence of the lingual valley on P_4 appear to be the most diagnostic features in differentiation of the taxa. The P_4 of *Diprionomys* is higher crowned than that of *Oregonomys* (Fig. 11), and the persistence of the lingual valley to the base of the tooth in *D. parvus* parallels the condition of the hypsodont geomyines.

One other species, *Diprionomys agrarius* Wood (1935:178) from Clarendonian deposits in Nebraska, resembles the species of *Oregonomys* more closely than does *D. parvus*. *D. agrarius* is large, has a low-crowned dentition, grooved upper incisors, a short lingual valley on P_4, and an expanded auditory region, and should, therefore, probably be assigned to *Oregonomys*. It differs from all other species of *Oregonomys* in possession of only three cusps on the metalophid of P_4 rather than five or six. The protoconid and metaconid of *O. agrarius* are at the extremities of the metalophid and are separated by a smaller cusp. Whether this cusp represents part of an anterior cingulid or an anteriorly positioned anteroconid cannot be determined, but the metalophid certainly has not attained the molariform appearance of the other species. Of course, the presence of *O. agrarius* in deposits of Clarendonian age and the possibility that the premolar represents a primitive stage from which that of the other species could be derived does not preclude *O. agrarius* from the ancestry of the other three species.

Korth (1979) noted that *Diprionomys agrarius* is most similar to *Halticosomys, nomen nudum,* which W. G. Reeder (1958) described in his University of Michigan dissertation in which he reviewed the Tertiary Heteromyidae. I concur with this designation, and although I have not seen the specimens Reeder described, I suspect they should be regarded as *Oregonomys.*

Oregonomys pebblespringsensis, new species

Holotype.—UWBM 57116, dentary with incisor, P_4–M_3, coronoid and articular processes intact.

Type locality.—UWBM locality C0127, Arlington 14.

Stratigraphic position.—Dalles Formation, *sensu lato* (Newcomb, 1971).

Age.—Hemphillian.

Referred specimens.—UWBM 57069, 5 upper incisors, one lower incisor; UWBM 57070, 6 upper incisors, 9 lower incisors; UWBM 57071, 2 upper incisors; UWBM 57072, 60 upper incisors, 23 lower incisors; UWBM 57073–57074, maxillaries with P^4–M^1; UWBM 57075–57076, maxillaries with P^4; UWBM 57077, maxillary with M^1–M^3; UWBM 57078–57079, maxillaries with M^2–M^3; UWBM 57080, 4 maxillaries (edentulous); UWBM 57081–57090, 57140, P^4; UWBM 57091, dP^4; UWBM 57092–57113, M^1 or M^2; UWBM 57114–57115, M^3; UWBM 57117–57118, dentaries with P_4; UWBM 57119, dentary with M_2–M_3; UWBM 57120–57123, P_4; UWBM 57124–57139, 57141–57143, M_1 or M_2; UWBM 57144–57149, M_3; from locality C0127, Arlington 14.

UWBM 56783, 2 upper incisors, 5 lower incisors; UWBM 56784, upper incisors, one lower incisor; from the conglomerate layer at locality B1533, Arlington 4.

UWBM 56797, upper incisor from the conglomerate layer at locality C0125, Arlington 12.

UWBM 56798, upper incisor; UWBM 56799, lower incisor from the conglomerate layer; UWBM 56800, 3 upper incisors, 3 lower incisors; from the top of the buff sandstones and siltstones; UWBM 56801, upper incisor; UWBM 56802, dentary with lower incisor, P_4; from the base of the red siltstone; locality B1532, Arlington 3.

UWBM 56817, 3 upper incisors, 2 lower incisors; UWBM 56818, 7 upper incisors, one lower incisor; UWBM 56816, maxillary with P^4–M^1; UWBM 56823–56824, P^4; UWBM 56825, M^1 or M^2; UWBM 56819–56822, lower incisors; UWBM 56826, dentary with P_4–M_1; UWBM 56827–56828, dentaries with P_4; UWBM 56829, P_4; UWBM 56830–56832, 56835, M_1 or M_2; UWBM 56833–56834, M_3; from the buff sandstones and siltstones at locality C0120, Arlington 7.

UWBM 56856, 3 upper incisors; UWBM 56857, 3 upper incisors, 2 lower incisors; from the buff sandstones and siltstones at locality C0121, Arlington 8.

UWBM 56863, 2 upper incisors; UWBM 56864, 2 upper incisors, one lower incisor; UWBM 56865, lower incisor; UWBM 56868, maxillary with P^4–M^1; UWBM 56869, maxillary with P^4; UWBM 56870, M^1 or M^2; UWBM 56871, dentary with lower incisor; UWBM 56872, dentary (edentulous); from the buff sandstones and siltstones; UWBM 56866, upper incisor; UWBM 56873, 7 upper incisors; UWBM 56867, maxillary with P^4–M^1; UWBM 56874–56875, maxillaries with M^1–M^3; UWBM 56876, maxillary (edentulous); UWBM 56877, P^4; UWBM 56880, lower incisor; UWBM 56878, dentary with P_4–M_3; UWBM 56881, dentary with P_4–M_2; UWBM 56879, dentary with P_4; from the base of the red siltstone; locality C0124, Arlington 11.

UWBM 56913, dentary with P_4–M_1 from the base of the red siltstone at locality C0123, Arlington 10.

UWBM 56916, upper incisor; UWBM 56914, auditory bulla; UWBM 56915, M_1 or M_2; from the base of the red siltstone at locality C0122, Arlington 9.

UWBM 56922, 4 upper incisors, one lower incisor; UWBM 56923, maxillary with M^1–M^3; UWBM 56924–56925, maxillaries (edentulous); UWBM 56926, M^1 or M^2; UWBM 56927, 3 upper incisors; UWBM 56928, lower incisor; UWBM 56929, dentary (edentulous) from reworked sandstones; UWBM 56930, 2 upper incisors from the conglomerate layer; locality C0126, Arlington 13.

UWBM 57068, upper incisor; UWBM 57067, P^4; UWBM 57065, P_4; UWBM 57066, M_1 or M_2; from locality C0141, Arlington 15.

UWBM 57038–57039, upper incisors; UWBM 57035, lower incisor; UWBM 57036, 2 upper incisors; UWBM 57037, M_1 or M_2 from the buff sandstones and siltstones; UWBM 57040, lower incisor; UWBM 57041, M_1 or M_2 from the base of the red siltstone; UWBM 57042, 3 upper incisors; UWBM 57043, maxillary with M^2–M^3; UWBM 57044, 3 lower incisors; UWBM 57045, dentary with incisor, P_4–M_2; UWBM 57046, dentary with M_1–M_3; from the top of the red siltstone; UO F-8302, partial skull (edentulous) from the red siltstone; locality B1534, Arlington 5.

UWBM 56637, 30 upper incisors; UWBM 56625–56626, maxillaries with P^4–M^3; UWBM 54376, 56627–56630, maxillaries with P^4–M^1; UWBM 54377, 56631–56633, maxillaries with P^4; UWBM 56634–56635, maxillaries with M^1–M^2; UWBM 56636, maxillary with M^1; UWBM 54396–54400, 56638–56661, P^4; UWBM 54401–54402, 56662–56676, 56696–56711, M^1 or M^2; UWBM 56712–56713, M^3; UWBM 56735, 15 lower incisors; UWBM 56714–56715, dentaries with P_4–M_1; UWBM 56716–56718, dentaries with P_4; UWBM 56720, dentary with M_1–M_3; UWBM 56721–56722, dentaries with M_1–M_2; UWBM 56723, dentary with M_2–M_3; UWBM 56724, dentary with M_2;

UWBM 56725, dentary with incisor; UWBM 54392, dentary (edentulous); UWBM 54389–54391, 56726–56734, 56736, 56746, P_4; UWBM 54383–54388, 56747–56778, M_1 or M_2; UWBM 56779–56782, M_3; from locality A8803, Ordnance.

Diagnosis.—P^4 with curved anterior profile of the protoloph, lophs connecting medially or lingually depending on the presence and position of an accessory cuspule on the metaloph, and hypostyle usually anteriorly located; lophs of upper molars initially connecting lingually, then buccally to encircle a medial fossette; protocone on M^3 small; dentary with prominent angular process not reaching the incisor capsule; P_4 with large, cuspate anteroconid, anterior cingulid originating from the metaconid and composed of small cuspules, small hypostylid, and deep anterior cleft between the anterior cingulid and the protoconid; lower molars with straight, transverse hypolophids, connecting buccally to protolophid.

Etymology.—Named for Pebble Springs, the closest landmark to the type area; Latin suffix *ensis* meaning native or resident in.

Description.—The posterior portion of a skull, UO F-8302 (Fig. 12, a, b) was collected by Shotwell and Avery in 1954 from the NW¼, sec. 31, T3N, R22E, UO locality 2323. This description covers three localities, UWBM locality C0122, C0123, and C0124, from which fossils were collected for this report. Matrix adhering to the skull indicates that it was collected from the red siltstone. Also from this horizon at Arlington 9, UWBM locality C0122, I collected a portion of an inflated mastoid, UWBM 56914. From these two specimens it can be observed that the auditory region was expanded similar to the condition of *Dipodomys.* Most of both bullae of UO F-8302 and the portion of the skull anterior to the parietals are broken away. The parietals are longer anteroposteriorly than those of *Dipodomys* and resemble more closely those of *Perognathus,* differing in longer posterior processes which project to the lateral sides of the interparietal. The interparietal of UO F-8302 is quadrate, does not extend as far laterally as that of *Perognathus parvus,* and is not nearly as reduced as that of *Dipodomys,* whose reduction, as Howell (1932:491) notes, is due to enlargement of the auditory region. Fragments of the inner wall of the right auditory region indicate that it extended half the distance from the rear of the skull to the anterior margin of the parietal and abutted against the laterocaudal edge of the parietal. Therefore, the size of the auditory portion of the skull of *Oregonomys* is more similar to that of *Dipodomys* than to that of *Perognathus.* This comparison is reinforced by UWBM 56914, an isolated specimen of a mastoid which is inflated and bipartite like that of *Dipodomys.* The primary differences distinguishing the mastoids of the two genera are the small size of the posterior segment of the mastoid, the smaller fossa for the paraflocculus, and the internal construction of the mastoid of *Oregonomys.* A labyrinthine construction of the mastoid of *Oregonomys* is formed by numerous supporting struts (Fig. 12, b), whereas the number of struts in the mastoid of *Dipodomys* is much fewer, resulting in large, empty caverns. Unlike those of *Perognathus* and other modern geomyid genera, the mastoids of *Oregonomys* and *Dipodomys* do not have thick, cancellous walls. The cochlea is preserved on UWBM 56914 and on UO F-8302 and resembles that of *Perognathus* and *Dipodomys* in axial length and medial constriction. The stapedial canal appears to have been only partially ossified, like that of *Perognathus,* not completely ossified as in *Dipodomys.* Therefore, the auditory region of *Oregonomys* possesses some features like those of *Perognathus,* such as incompletely ossified stapedial canal, large interparietal, and small indentation for the paraflocculus, but possesses large, inflated mastoids with noncancellous walls, similar to the condition of *Dipodomys.*

The upper incisor of *Oregonomys* is larger, but curved, medially grooved, and has a short wear facet like that of *Perognathus.* The sulcate upper incisors contrast with the smooth anterior face on the incisor of *Perognathoides quartzus* Hall from Clarendonian deposits in Nevada.

As documented by many dentulous maxillaries (Fig. 12), *Oregonomys pebblespringsensis* is characterized by a wide palate with parallel tooth rows, a brachyodont dentition, and a decrease in the width of the cheek teeth posteriorly. However, the reduction of width of the cheek teeth is not as great as that of all species of *Perognathoides.* The anterior root of the zygomatic arch arises opposite or just anterior to P^4 and is dorsoventrally deep, indicating a broad masseteric fossa. On the palate, three ridges originate just posterior to the incisive foramina. The two lateral ridges continue posteriorly and merge with the elevated portion of the maxillary, which houses the cheek teeth, and the medial ridge persists back and gradually fades between the posterior borders of the premolars. With tooth wear, lingual union of the lophs of M^3 occurs first, usually followed in a succession anteriorly, but sometimes union of the lophs of the P^4 occurs secondly. With wear, the oc-

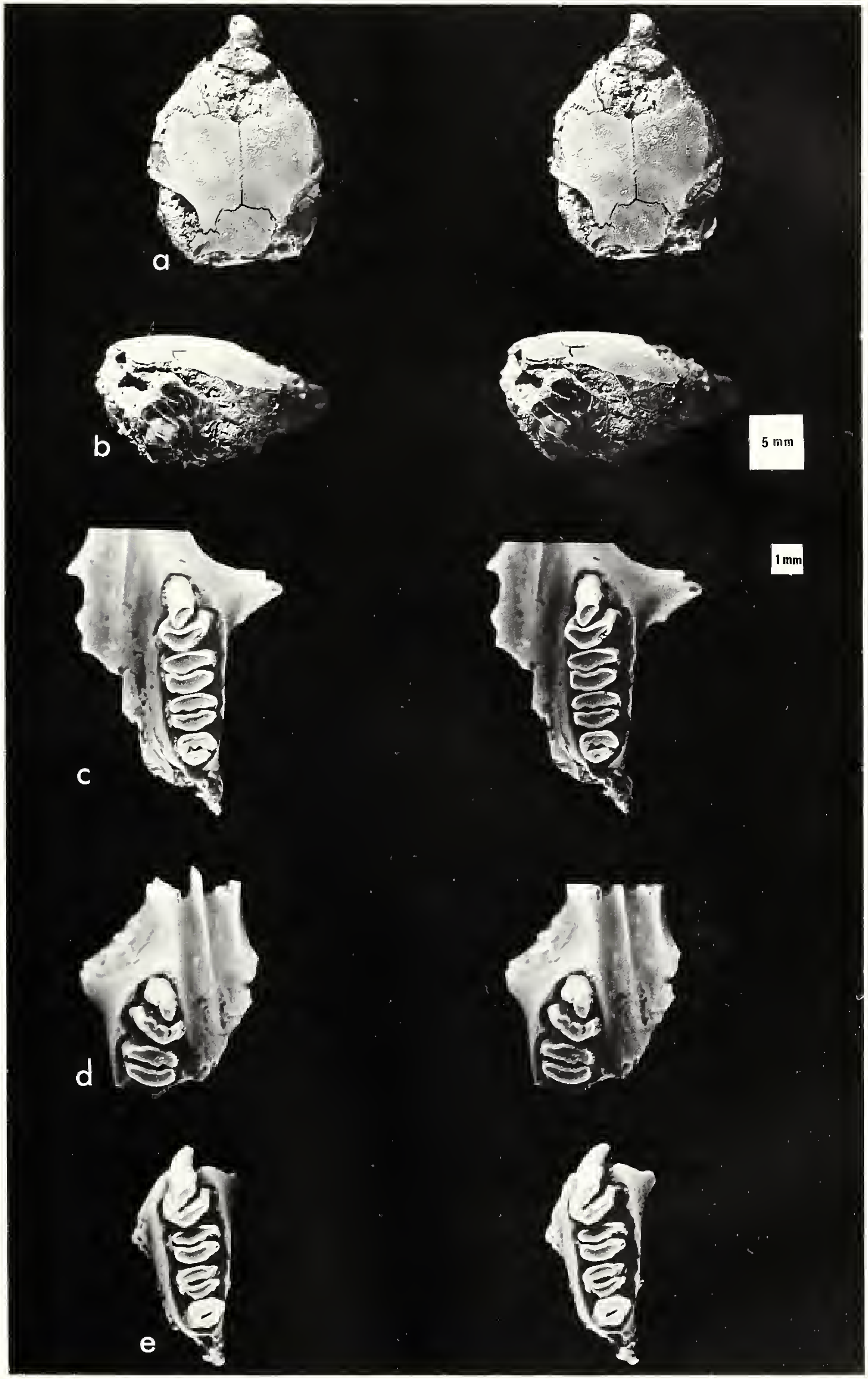

Fig. 12.—Selected specimens of *Oregonomys pebblespringsensis.* a) UO F-8302, skull, dorsal view; b) UO F-8302, skull, right lateral view; c) UWBM 56625, left maxillary with P^4–M^3; d) UWBM 56816, right maxillary with P^4–M^1; e) UWBM 56626, left maxillary with P^4–M^3. Scale equals one millimeter.

Table 8.—*Measurements of* Oregonomys pebblespringsensis *at different wear stages*[1] *from the Ordnance locality.*

Tooth and measurement	N	Observed range	Mean	S	CV
P^4: unworn					
AP	9	1.05–1.7	1.33 ± .16	.21 (.14–.40)	15.91 ± 7.35
T	9	1.2–1.7	1.42 ± .13	.17 (.12–.33)	12.07 ± 5.58
P^4: moderately worn					
AP	11	1.2–1.55	1.40 ± .07	.11 (.08–.19)	7.92 ± 3.31
T	11	1.25–1.65	1.47 ± .09	.14 (.10–.25)	9.40 ± 3.93
P^4: worn					
AP	10	1.45–1.8	1.58 ± .07	.10 (.07–.18)	6.54 ± 2.87
T	9	1.5–1.85	1.65 ± .08	.10 (.07–.19)	6.25 ± 2.89
M^1 or M^2: unworn					
AP	16	1.0–1.35	1.17 ± .06	.11 (.08–.17)	7.60 ± 2.63
T	16	1.2–1.65	1.46 ± .06	.11 (.08–.17)	7.32 ± 2.54
M^1 or M^2: moderately worn					
AP	13	1.0–1.3	1.19 ± .06	.10 (.07–.17)	8.61 ± 3.31
T	13	1.25–1.7	1.46 ± .08	.13 (.09–.21)	9.18 ± 3.53
M^1 or M^2: worn					
AP	17	1.1–1.4	1.23 ± .05	.09 (.07–.14)	7.58 ± 2.55
T	17	1.2–1.8	1.59 ± .08	.15 (.11–.23)	9.61 ± 3.23
P_4: unworn					
AP	9	1.0–1.4	1.17 ± .11	.14 (.10–.27)	12.12 ± 5.60
T	9	.85–1.36	1.10 ± .14	.18 (.12–.35)	16.06 ± 7.42
P_4: moderately worn					
AP	16	1.05–1.25	1.17 ± .06	.12 (.09–.19)	9.94 ± 3.44
T	13	.90–1.3	1.14 ± .06	.10 (.07–.17)	8.70 ± 3.34
P_4: worn					
AP	4	1.15–1.3	1.24 ± .10	.06 (.03–.22)	5.08 ± 3.52
T	4	1.0–1.25	1.16 ± .18	.11 (.06–.41)	9.54 ± 6.61
M_1 or M_2: unworn					
AP	19	.95–1.45	1.25 ± .06	.13 (.10–.19)	10.58 ± 3.36
T	19	1.15–1.6	1.36 ± .07	.14 (.11–.21)	9.99 ± 3.18
M_1 or M_2: moderately worn					
AP	16	1.2–1.4	1.30 ± .04	.08 (.06–.12)	5.79 ± 2.01
T	16	1.35–1.65	1.52 ± .04	.08 (.06–.12)	5.34 ± 1.85
M_1 or M_2: worn					
AP	12	1.2–1.45	1.33 ± .06	.09 (.06–.15)	6.70 ± 2.68
T	12	1.4–1.7	1.51 ± .06	.10 (.07–.17)	6.90 ± 2.76

[1] Wear stages as follows: (1) unworn—cusps discernible; (2) moderately worn—loph union has occurred; and (3) worn—loph union across half or more of the occlusal surface.

clusal dimensions of the cheek teeth change as illustrated by Table 8, particularly those of the premolars.

The protoloph of the upper premolars exhibits a low population variability, but the metaloph shows a wide range of variation. On all but 1 of 64 known specimens, the protoloph is composed of a large, columnar protocone, which dominates a smaller, buccal cuspule. The two cusps unite during the course of wear to form an ellipse-shaped occlusal surface, which is oriented obliquely with the buccal margin farther away from the metaloph. This contrasts with the species of *Perognathoides,* which have a bilaterally symmetrical protoloph connecting medially to the metaloph. UWBM 57074 has two accessory cuspules on the buccal side of the protocone and an enamel bulge on the posterior side, but with wear the same occlusal pattern of the other premolars would emerge. The anterior face of all premolars of *O. pebblespringsensis* is curved downward; there is

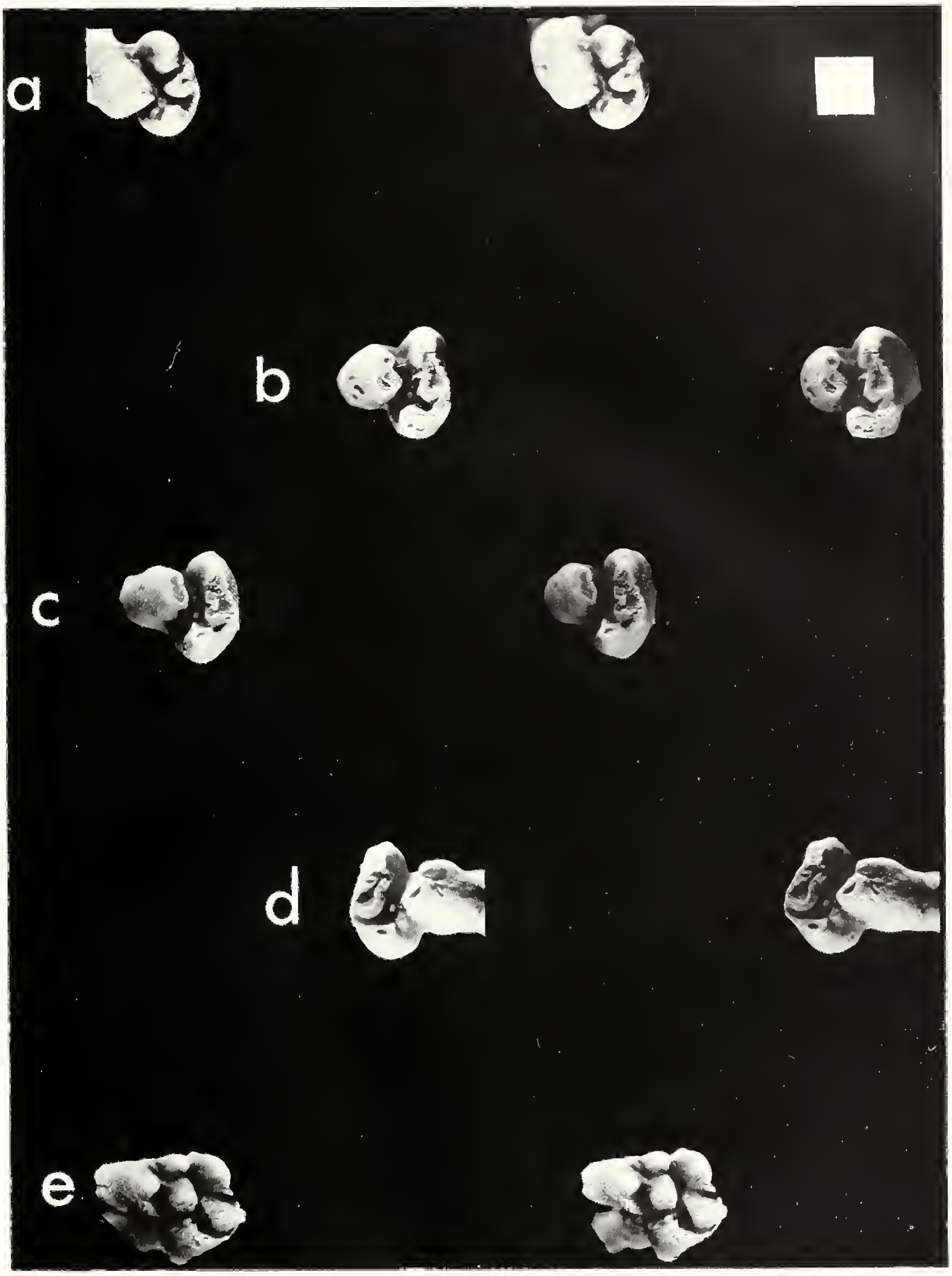

Fig. 13.—Selected teeth of *Oregonomys pebblespringsensis*. a) UWBM 56652, left P^4; b) UWBM 56641, left P^4; c) UWBM 56659, left P^4; d) UWBM 56645, right P^4; e) UWBM 57901, left dP^4. Buccal is to the top; scale equals one millimeter.

not constant slope of the anterior profile. The position of the hypostyle ranges from a position in line with the metaloph, as on UWBM 56652 (Fig. 13, a) and 56653, to a position perpendicular to the metaloph. On all specimens that exhibit anterior displacement of the hypostyle, it connects to the lingual corner of the hypocone by a short, posterior cingulum. The metacone and hypostyle are subequal and smaller than the hypocone. The most variable feature of the metaloph, and one which determines the manner of loph connection of P^4, is the presence or absence, position, and size of a small cuspule. If

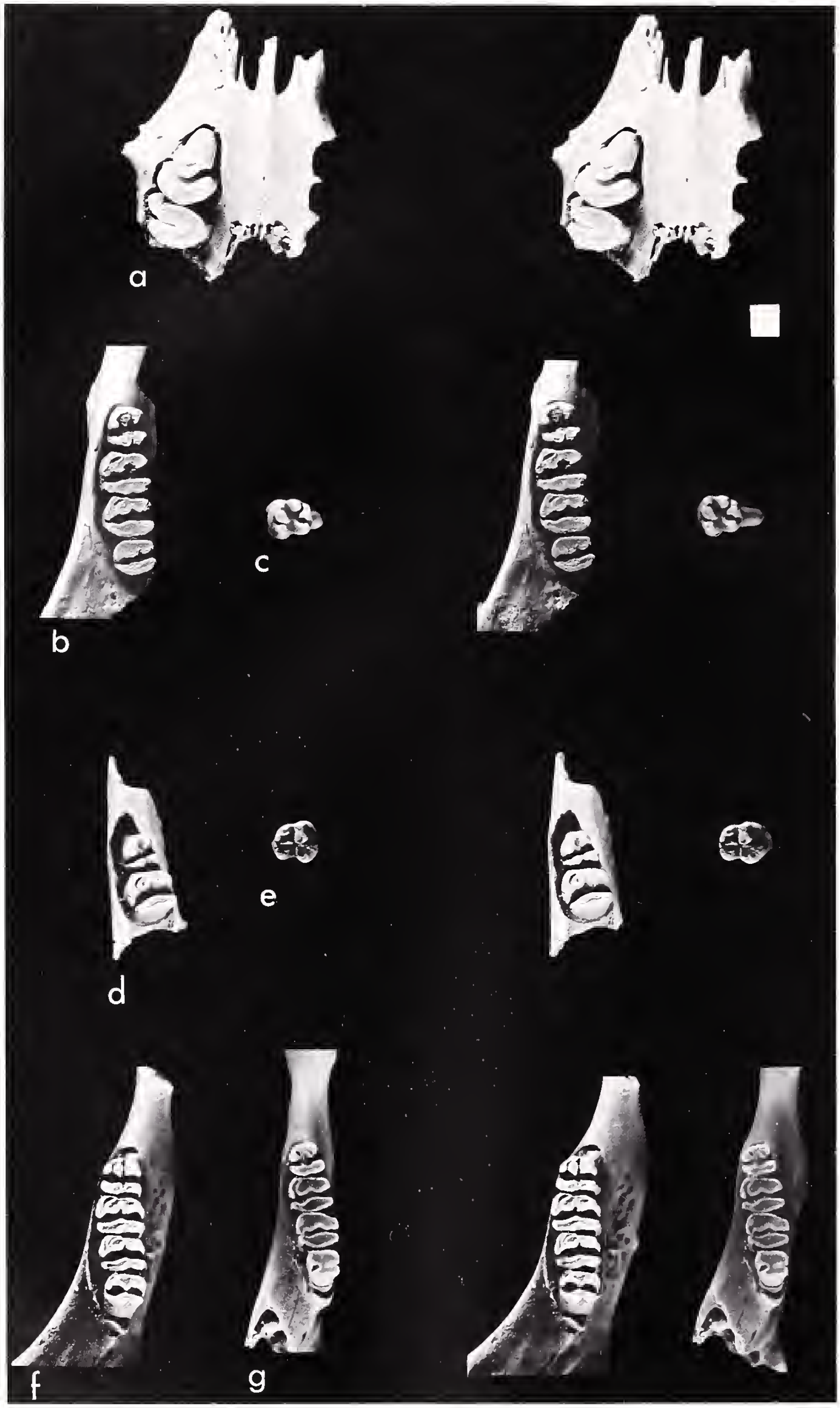

Fig. 14.—Selected specimens of some species of *Oregonomys*. a) *O. sargenti*, UWBM 57779, right maxillary with P^4–M^1; b) *O. pebblespringsensis*, UWBM 57116, left dentary with P_4–M_3 (holotype); c) *O. pebblespringsensis*, UWBM 56729, left P_4; d) *O. pebblespringsensis*, UWBM 56714, left dentary with P_4–M_1; e) *O. pebblespringsensis*, UWBM 56726, right P_4; f) *O. sargenti*, UO F-3637, left dentary with P_4–M_3 (holotype); g) *O. magnus*, SDSM 8749, left dentary with P_4–M_3. Scale equals one millimeter. Buccal is to the top on isolated teeth.

the cuspule is absent, the lophs remain separate until very late wear stages when they unite medially (Fig. 12, c). When the cuspule is present, it is normally between the hypostyle and hypocone on the anterior side of the metaloph. Although it can be attached to either major cusp and sometimes bridges both, the cuspule usually arises from the base of the hypostyle (Fig. 13, a, b, c) causing wear to unite the metaloph and protoloph at their lingual extremities (Fig. 12, e; Fig. 13, d). Therefore, the variable position of the cuspule results in initial loph connection ranging from lingual to medial. From the Arlington localities, only 7 of 21 specimens exhibit an accessory cuspule, while half of the sample from Ordnance possesses a cuspule. This difference might reflect the smaller sample from the Arlington localities or could represent a slight temporal difference.

Some specimens of P^4 exhibit other variations of the position of the cuspule. UWBM 57074 has a newly erupting P^4 followed by an M^1 on which the cusps have been worn away, but lingual union has not occurred. In this specimen the cuspule is between the hypostyle and hypocone, and with little wear it would soon be indistinguishable. Therefore, the cuspule might have been present on moderately worn specimens, but incorporated into the metaloph. Other variations include UWBM 56868, which possesses two cuspules between the hypocone and metacone on the anterior and posterior margins of the metaloph, enclosing a small fossette. On UWBM 56877 a cuspule exists on the posterior edge of the metaloph between the metacone and hypocone, and many worn specimens have an enamel bulge on the anterior side of the metacone which might represent this cuspule. There appears to be no correlation between the presence or position of cuspules and the position of the hypostyle.

Three roots, two beneath the metaloph, are well developed on P^4 before occlusal wear. Only two roots are normally present on the P^4 of *Diprionomys parvus* (Shotwell, 1967:15). The crown pattern of an isolated dP^4, UWBM 57091 (Fig. 13, e), resembles that of the deciduous premolars illustrated by Wood (1935:219) for the pocket mice. Instead of the Y-shaped configuration characteristic of the posterior loph of the dP^4 of *Parapliosaccomys* and the metaloph of the upper molars of other geomyines (a characteristic which seems consistent; the identity of the posterior loph of a deciduous premolar and the posterior loph of the molar), UWBM 57091 has three cusps arranged in a transverse line. The central cusp on this loph is displaced anteriorly as is the hypocone of the upper molars of *Oregonomys,* and the loph is connected lingually to the bicusped medial loph. The anterior loph, which remains separate from the other lophs after wear, consists of a major cusp flanked lingually by a cuspule and buccally by an enamel shelf.

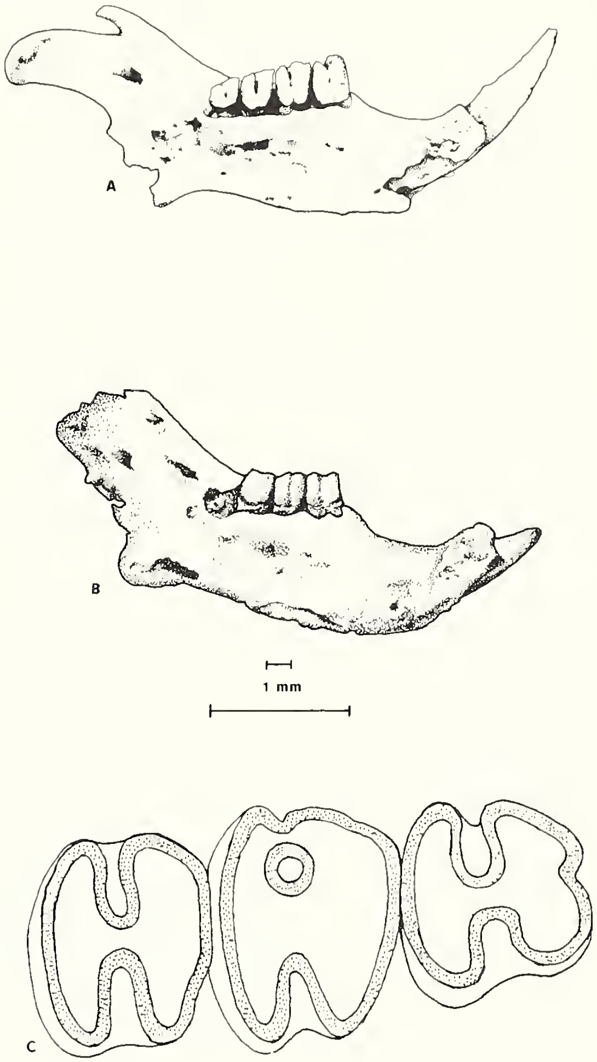

Fig. 15.—Left dentary of *Oregonomys pebblespringsensis* (A), UWBM 57116 (holotype), compared with the same element in *O. sargenti* (B), UWBM 57778, with occlusal view of the latter (C).

The upper molars are conservative in their construction. They are suboval in outline and, with wear, their lophs unite first at the lingual margin and then at the buccal extremity of the molars, forming a fossette from the transverse valley. The fossette appears first on the M^3, but can be next formed on

Table 9.—*Types of connections of the lophids of* P_4 *in* Oregonomys.

Connection type	Arlington	Ordnance	McKay	Hagerman
Medial	1	4	0	0
Medial then buccal	4	15	1	1
Buccal then medial	2	3	0	0

either M^1 or M^2. It is difficult to differentiate between isolated specimens of M^1 and M^2, although the lophs of M^1 are normally more curved, the anterior cingulum is better developed and isolates the protocone, and the inflection of the hypostyle is more pronounced, resulting in a square posterolingual corner. The first two molars have three roots; two beneath the buccal margin and one beneath the lingual edge.

Specimens of M^3 from Ordnance differ in root formation from those collected at Arlington. All third molars have three roots, but those from Ordnance have convergent roots, whereas those from Arlington have widely divergent roots. Based on a total of three specimens from both regions on which roots can be observed, I hesitate to put much reliance on the characteristic, particularly since it occurs on the last tooth in the row, a most variable molar.

Many of the dentaries are well preserved, possess a complete dentition, and are constructed similar to those of extant taxa of pocket mice. The holotype of *O. pebblespringsensis,* UWBM 57116 (Fig. 14, b; Fig. 15, A), is extraordinarily well preserved with the coronoid and articular processes, incisor, and complete and unworn adult dentition intact. Only a portion of the angular process is broken away. In this specimen and numerous others the mental foramen is situated below the diastema and anterior to the masseteric scar as is characteristic of *Heteromys* and *Liomys.* The mandibular symphysis of *O. pebblespringsensis* ends below the midpoint of the diastema, forming a curved ventral margin of the dentary unlike the highly angulate dentary of the Recent geomyines. There is no well defined dorsal crest for insertion of *M. masseter medialis, pars anterior* on the dentary of *O. pebblespringsensis,* and the ventral ridge terminates below P_4 just ahead of its anterior root and ventral to the midpoint of the mandibular depth. From this point the lower masseteric crest descends to near the ventral margin of the dentary, continues posteriad as a horizontal line, and fades below M_3, similar to the condition of *Liomys* and *Heteromys,* although their masseteric ridges descend at a greater angle. On UWBM 57116, UWBM 56881, and UWBM 57046, structure of the ascending ramus appears most like that of *Perognathus* and *Liomys,* but shows some similarities to *Dipodomys.* The coronoid process, for example, is deflected laterally more than that of *Perognathus* or *Liomys,* but not to the degree exhibited by *Dipodomys,* indicating expansion of the auditory region on the skull of *O. pebblespringsensis.* As noted for the skull and reflected by development of the angular process, the inflation of the auditory region resembles that of *Dipodomys,* but has not progressed as far. On *Dipodomys* the angular process is greatly expanded, flares laterally, and extends up to the incisor capsule, whereas that of *O. pebblespringsensis* is less expanded and is more similar to that of *Perognathus,* in which the dorsal edge of the process lies well below the incisor capsule. The dental foramen lies on the incisor trace below the bifurcation of the articular and coronoid processes. The alveoli of the anterior molars are double-rooted and well divided, but those of M_3 are shallow, so the M_3 is seldom found inserted. Therefore, the ramus of the dentary has characteristics which typify species of the Heteromyinae, but the ascending ramus displays morphological characteristics which resemble those of *Dipodomys* and *Perognathus.*

The lower incisor of *O. pebblespringsensis* is gently curved and flattened on the medial side. Although larger than those of *Diprionomys parvus,* these incisors are similar in that the enamel curves around the anterior face and ends almost midway on the lateral side, usually farther than on Recent species of pocket mice. The distal terminus of the lower incisor of *O. pebblespringsensis* is in a well formed incisor capsule, constructed most like that of *Liomys.*

The cheek teeth are brachyodont and are heavily constructed like those of *Liomys.* As demonstrated by UWBM 56714 (Fig. 14, d), before the P_4 has fully erupted, all of the cusps on M_1 are worn and connected on each lophid. In a later wear stage, as exemplified by the type specimen, the cusps on the hypolophid of P_4 are united, but those on the metalophid are untouched, and the lophids of the molars are worn to transverse crests. When wear does occur on the metalophid of P_4, as on UWBM 57045, the molar lophs remain separate, but tend to unite medially and buccally to form a buccal fossette. When a buccal and a medial connection form on the P_4, only a lingual indentation remains on the molars as exemplified by UWBM 56913. Measurements of the premolars and molars from the Ordnance locality at different wear stages are presented in Table 8.

The premolar on the type specimen (Fig. 14, b) illustrates the basic configuration of the P_4 of *O. pebblespringsensis.* The metalophid is composed, lingually to buccally, of a large, high protoconid, a distinct anteroconid, and a metaconid from which an anterior cingulid originates, extends around the anterobuccal corner of the P_4, and terminates opposite the protoconid. The cingulid is separated from the protoconid by a deep, anterior cleft. The cingulid is composed of one or two minute cuspules and mirrors the anterobuccal cingulid of the molars. Sometimes when two cuspules exist, as on UWBM 56726 (Fig. 14, e), the cingulid merges with the protoconid so no anterior cleft remains. UWBM 54391 and 56727 have an additional cuspule anterior to the protoconid. With wear a buccal connection between the metaconid and hypostylid and a medial connection between the hypoconid and anteroconid, a cusp which is normally isolated internally, would appear at about the same time. However, like the upper premolar, the lower has a range of connections of the lophids from central, to central then buccal, to buccal then medial, and the point of connection is also dependent upon the variation of a single cusp, in this case, the anteroconid. If the anteroconid is absent like that on UWBM 56729 (Fig. 14, c), or incipient like that on UWBM 56726 and 56730, the metalophid and hypolophid first meet buccally, then medially. A large anteroconid sometimes results in a medial connection followed by a buccal connection, but sometimes, as on UWBM 57118, a medial connection persists. Table 9 illustrates the distribution of the types of connections from the different localities.

In contrast to the wide variability of the metalophid of P_4, the hypolophid is more conservatively constructed, consisting of three cusps arranged in a transverse crest. Only the hypostylid, which is often so small that the posterior lophid appears bicuspid, displays any variation.

The three lower molars are similar, except for minor differences such as size (Table 10) and development of the anterobuccal cingulid. The M_1 is normally the largest tooth, has a more angular cingulid than M_2 or M_3, squaring the anterobuccal corner, and the roots normally diverge greatly. The occlusal outline of M_2 is oval, and the roots are close together, sometimes fused throughout much of their length. Union of the lophids after wear is at the buccal margin, although a few teeth, particularly third molars, show tendencies for medial connection followed by a buccal union. This tendency on M_3 is the result of the anterior position of the protostylid, which produces a shorter cingulid than is present in M_1 or M_2. Similarities between the molars include: bulbous cusps, a transverse, crest-shaped hypolophid, and a metalophid, which has a nearly isolated protoconid and an anterobuccal cingulid originating from the protostylid.

Oregonomys sargenti (Shotwell)

Perognathus sargenti Shotwell, 1956:730–731; 1967:12–13.

Holotype.—UO F-3637, dentary with P_4–M_3.

Type locality.—UWBM locality C0128 (equals UO locality 2222), McKay Reservoir.

Stratigraphic position.—Dalles Formation, *sensu lato* (Newcomb, 1971).

Age.—Hemphillian.

Referred specimens.—UWBM 57777, upper incisor; UWBM 57779, maxillary with P^4–M^1; UWBM 57780, M^1; UWBM 57781, M^2; UWBM 57778, dentary with P_4–M_2; UWBM 57973, maxillary with P^4–M^1; UWBM 57974, isolated M^1 and M^2; UWBM 57975, M^3; UWBM 57976, dentary with M_1–M_3; UWBM 57977, M_1 or M_2; UWBM 57978, M_3 from locality C0128, McKay Reservoir.

Preservation.—UWBM 57973–57978 include specimens of a single individual preserved in a coprolite with specimens of *Perognathus, sensu stricto.* All others were obtained by surface prospecting, hand breaking, or washing.

Amended diagnosis.—Anterior profile of P^4 uncurved; protoloph of P^4 assuming trapezoidal occlusal surface with narrow anterior end; hypostyle in line with metaloph on P^4, and no lingual connection of lophs on available specimens; lophs of M^1 connecting medially and lingually at about the same time unlike *O. pebblespringsensis*; lophs of M^2–M^3 connecting lingually first, then buccally, forming medial fossettes; small protocone on M^3 unlike *O. magnus*; angular process on dentary large, extending near incisor capsule; P_4 extremely molariform; large, cuspate anteroconid unlike *O. magnus,* anterior cingulid crest-shaped, originating from the mesoconid; deep anterior cleft unlike *O. magnus*; double medial connection of lophids on P_4 unlike *O. pebblespringsensis*; large hypostylid forming a wide hypolophid on P_4; lophids of lower molars connecting medially unlike *O. magnus*; hypolophid on M_1 and M_2 angulate.

Description.—This collection includes the first known upper teeth of this species, including the up-

Table 10.—*Measurements of* Oregonomys pebblespringsensis.

Museum no.	Specimen	AP	T
Locality C0123			
UWBM 56913,	dentary with P_4	1.2	1.3
	M_1	1.3	1.5
Locality C0122			
UWBM 56914,	M_1 or M_2	1.35	1.4
Locality C0126			
UWBM 56923,	maxillary with M^1	1.35	1.55
	M^2	1.15	1.45
	M^3	.95	1.15
UWBM 56926,	M^1 or M^2	1.35	1.4
Locality C0141			
UWBM 57067,	P^4	1.15	1.2
UWBM 57065,	P_4	1.0	1.03
UWBM 57066,	M_1 or M_2	1.12	1.4
Locality C0120			
UWBM 56816,	maxillary with P^4	1.4	1.5
	M^1	1.3	1.7
UWBM 56824,	P^4	1.45	1.6
UWBM 56825,	M^1 or M^2	1.25	1.4
UWBM 56826,	dentary with P_4	1.25	1.3
	M_1	1.35	1.7
UWBM 56827,	P_4	1.2	1.3
UWBM 56828,	P_4	1.3	1.3
UWBM 56829,	P_4	1.15	1.35
Locality C0120			
UWBM 56830,	M_1 or M_2	1.4	1.5
UWBM 56831,	M_1 or M_2	1.3	1.4
UWBM 56832,	M_1 or M_2	1.3	1.6
UWBM 56833,	M_3	1.15	1.35
UWBM 56834,	M_3	1.15	1.4

Tooth and measurement	N	Observed range	Mean	S	CV
Locality C0124					
P^4, AP	3	1.35–1.7	1.58 ± .40	.16 (.08–1.0)	10.15 ± 8.12
T	4	1.35–1.65	1.5 ± .27	.17 (.10–.63)	11.55 ± 8.00
M^1 or M^2, AP	6	1.05–1.4	1.22 ± .13	.12 (.08–.30)	9.95 ± 5.63
T	6	1.4–1.5	1.49 ± .10	.09 (.06–.22)	6.15 ± 3.48
M^3, AP	2	.95–1.0	.98 ± .36	.04 (.02–1.28)	3.63 ± 3.56
T	2	1.05–1.15	1.10 ± .63	.07 (.03–2.23)	6.43 ± 6.30
P_4, AP	3	1.2–1.45	1.3 ± .32	.13 (.07–.82)	10.18 ± 8.15
T	3	1.15–1.3	1.22 ± .20	.08 (.04–.5)	6.28 ± 5.03
M_1 or M_2, AP	4	1.2–1.45	1.34 ± .18	.11 (.06–.41)	8.29 ± 5.75
T	4	1.45–1.6	1.51 ± .10	.06 (.04–.22)	4.16 ± 2.88
Locality C0127					
P^4, AP	15	1.3–1.8	1.49 ± .08	.15 (.11–.24)	10.14 ± 3.63
T	15	1.3–1.7	1.48 ± .07	.12 (.09–.19)	7.99 ± 2.86
M^1 or M^2, AP	27	.95–1.4	1.22 ± .08	.12 (.10–.17)	10.11 ± 2.70
T	26	1.25–1.8	1.52 ± .06	.15 (.12–.21)	9.73 ± 2.65
M^3, AP	5	.95–1.1	1.04 ± .09	.07 (.04–.20)	6.27 ± 3.89
T	5	1.2–1.3	1.27 ± .06	.05 (.03–.14)	3.52 ± 2.18
P_4, AP	7	1.1–1.45	1.22 ± .11	.12 (.08–.26)	9.42 ± 4.94
T	7	1.05–1.45	1.25 ± .12	.13 (.08–.29)	10.07 ± 5.28

Table 10.—*Continued.*

Tooth and measurement	N	Observed range	Mean	S	CV
M_1 or M_2, AP	22	1.2–1.45	1.3 ± .03	.07 (.05–.10)	5.57 ± 1.65
T	21	1.25–1.7	1.42 ± .08	.11 (.08–.16)	7.58 ± 2.29
M_3, AP	8	1.0–1.2	1.075 ± .08	.09 (.06–.18)	8.25 ± 4.04
T	8	1.1–1.35	1.225 ± .07	.08 (.05–.16)	6.17 ± 3.02
			Locality A8803		
P^4, AP	38	1.0–1.8	1.42 ± .06	.18 (.15–.23)	12.53 ± 2.82
T	37	1.2–1.85	1.49 ± .05	.16 (.13–.21)	10.91 ± 2.49
M^1 or M^2, AP	46	1.0–1.4	1.20 ± .03	.10 (.08–.13)	8.65 ± 1.77
T	46	1.25–1.8	1.51 ± .04	.14 (.12–.18)	9.56 ± 1.95
M^3, AP	4	.90–1.0	.96 ± .08	.05 (.03–.19)	4.97 ± 3.44
T	4	1.1–1.3	1.21 ± .14	.09 (.05–.34)	7.04 ± 4.88
P_4, AP	27	1.0–1.4	1.17 ± .04	.11 (.09–.15)	9.18 ± 2.45
T	27	.85–1.36	1.14 ± .06	.14 (.11–.19)	12.04 ± 3.21
M_1 or M_2, AP	47	.95–1.5	1.28 ± .03	.11 (.09–.14)	8.53 ± 2.28
T	47	1.2–1.7	1.45 ± .04	.14 (.12–.18)	9.28 ± 1.88
M_3, AP	6	.80–1.2	1.08 ± .16	.15 (.09–.37)	14.03 ± 7.94
T	6	1.0–1.3	1.18 ± .10	.09 (.06–.22)	7.49 ± 4.24

per and lower dentition of a single individual. Except for the morphology of P^4 and the manner of connection of lophs of M^1, the upper cheek teeth and incisor are similar to those of *O. pebblespringsensis.* The protoloph of the P^4 of *O. sargenti* is large and wears to a trapezoidal outline forming a larger surface area (Fig. 14, a) than on the elliptical protoloph of *O. pebblespringsensis.* Like that of *Thomomys* and some species of *Perognathus,* and unlike that of *O. pebblespringsensis* and *Oregonomys magnus* (Zakrzewski), the anterior slope of the protoloph of the P^4 of *O. sargenti* is straight to the tooth base. The two lophs on the P^4 of the species from McKay Reservoir remain separate until very late wear stages when medial union occurs. The metaloph on available specimens of the upper premolar of *O. sargenti* differs from that of *O. pebblespringsensis* in the absence of both accessory cuspules and the anterior inflection of the hypostyle. The medial valleys of the upper molars on some specimens of *O. sargenti* may be narrower than those of *O. pebblespringsensis.*

In deflection of the coronoid process and prominent incisor capsule the dentaries of the two species are identical; however, the articular process of the dentary of *O. sargenti* is slightly more inflected medially, and the angular processes on the type specimen and UWBM 57778 (Fig. 15, B) appear to have risen higher than the corresponding processes on *O. pebblespringsensis.* These characteristics might point to an even more greatly expanded auditory region on *O. sargenti* than on *O. pebblespringsensis.*

Descriptions of the type specimen by Shotwell (1956, 1967) illustrate the unworn lower dentition (Fig. 14, f). The additional specimens found in the coprolite and UWBM 57778 exemplify the occlusal morphology after wear. Particularly, UWBM 57778 clearly indicates that the lophids on the cheek teeth meet medially (Fig. 15, C). The M_1 has a prominent central union and a smaller buccal connection of the lophids, while those of P_4 and M_2 have only a medial connection. The latter two teeth are almost identical except that the metalophid of the P_4 is shorter transversely as indicated by Table 11 and retains an anterior notch between the anteroconid and protoconid. With additional wear a buccal connection of the lophids would occur on P_4, like that on M_1. The P_4 is very molariform in a worn state, and as UO F-3637 indicates, morphology of the unworn premolar is very similar to that of the molars. The anterobuccal cingulid and metaconid closely resemble the anterobuccal cingulid and protostylid of the molars, the anteroconid corresponds to the protoconid, and the protoconid of P_4 is the analogue of the metaconid on the molars. A distinctive feature of P_4 is a double medial connection of the lophids. Two crests, one from the anteroconid and one from the protoconid, join the hypoconid and entoconid, respectively. Only a single crest joins the midpoints of the lophids on the molars.

Table 11.—*Measurements of* Oregonomys sargenti.

Museum no.	Specimen	AP	T
UWBM 57779,	maxillary with P^4	1.55	1.7
	M^1	1.35	1.65
UWBM 57780,	M^1	1.25	1.4
UWBM 57781,	M^2	1.05	1.45
UWBM 57778,	dentary with P_4	1.25	1.4
	M_1	1.25	1.6
	M_2	1.15	1.6
UWBM 57782-3,	maxillary with P^4	1.35	1.4
	M_1	1.25	1.4
UWBM 57782-6,	M^1	1.2	1.4
UWBM 57782-6,	M^2	1.2	1.4
UWBM 57782-17,	M^3	.9	1.15
UWBM 57782-11,	dentary with M_1	1.4	1.45
	M_2	1.35	1.4
	M_3	1.15	1.2
UWBM 57782-26,	M_1 or M_2	1.35	1.4
UWBM 57782-24,	M_3	1.2	1.25

Because there is a great tendency for medial union of the lophids, the lower molars have some differences compared with those of *O. pebblespringsensis.* In particular, the middle cusp on each lophid of the molars of *O. sargenti* is expanded to fill the transverse valleys. The anterior edge of the hypoconid is especially enlarged, pointed, and gives the hypolophid a more angular anterior border than that of *O. pebblespringsensis.*

The M_3 of the type specimen is unique in that a medial union of the lophids is almost formed when the tooth is unworn. However, the specimens of M_3 preserved in the coprolite have well divided lophids like those of *O. pebblespringsensis.* Therefore, UO F-3637 may indicate the initiation of a tendency for central union of the lophids on M_3, but the species sometimes retains the configuration of *O. pebblespringsensis.*

Oregonomys magnus (Zakrzewski)

Perognathus magnus Zakrzewski, 1969:11–12.

Type specimen.—UMMP V55958, maxillary with P^4–M^3.

Type locality.—UM-Ida. 1a-65; sec. 32, T8S, R13E.

Stratigraphic position.—Glenns Ferry Formation.

Age.—Blancan; from the Hagerman fauna.

Referred specimens.—SDSM 8749, dentary with P_4–M_3; UMMP V53563, dentary with P_4–M_2 (worn); from UM-Ida. 1a-65 in Idaho.

Amended diagnosis.—Smaller than *O. pebblespringsensis* or *O. sargenti*; anterior profile of P^4 abbreviated unlike *O. sargenti,* hypostyle strongly inflected, lophs connecting lingually, and accessory cuspules absent on metaloph of P^4; lophs connecting medially on M^1; lophs connecting lingually and buccally, forming medial fossettes on M^2–M^3; protocone on M^3 large; anteroconid small and crest-shaped on P_4, deep anterior cleft absent and anterior cingulid on P_4 composed of two cuspules connecting to protoconid, not to metaconid; double medial connection of lophids on P_4; hypostylid of P_4 larger than that of *O. pebblespringsensis,* but smaller than that of *O. sargenti*; hyplophid transversely straight on M_1–M_2 with no anterior angulation and lophids connecting buccally; valley between the anterior cingulid and protoconid of M_1 remaining longer than on other species; lophids of M_3 connecting medially.

Table 12.—*Measurements of* Oregonomys magnus.

Museum no.	Specimen	AP	T
UMMP V55958,	P^4	1.32	1.50
	M^1	1.10	1.61
	M^2	1.02	1.42
	M^3	.90	1.19
UMMP V53565,	P_4	.97	1.03
	M_1	1.25	1.41
	M_2	1.20	1.38
SDSM 8749,	P_4	1.0	.98
	M_1	1.11	1.37
	M_2	1.11	1.32
	M_3	.82	1.08

Description.—Specimens of *O. magnus* are smaller (Table 12) than those of *O. sargenti* or *O. pebblespringsensis.* For example, the alveolar distance of the lower cheek teeth of SDSM 8749 is 4.8 mm, whereas that of the type specimens of *O. pebblespringsensis* and *O. sargenti* is 5.75 and 5.26 mm, respectively.

The holotype, UMMP V55958, represents the only known upper cheek teeth of *O. magnus* and displays some unique features. Loph connection on P^4 is lingual, unlike that of *O. sargenti,* and does not involve a cuspule on the metaloph like that of *O. pebblespringsensis.* The hypostyle is strongly inflected anteriorly to form a prominent lingual union, and the protoloph has a curved anterior profile unlike that on specimens of *O. sargenti.* In contrast to the condition on both species from Oregon, the lophs on the M^1 of *O. magnus* tend to unite medially. Lophs on M^2–M^3 connect lingually and subsequently unite buccally to enclose a medial fossette. The M^3, however, is distinctive because it displays a very

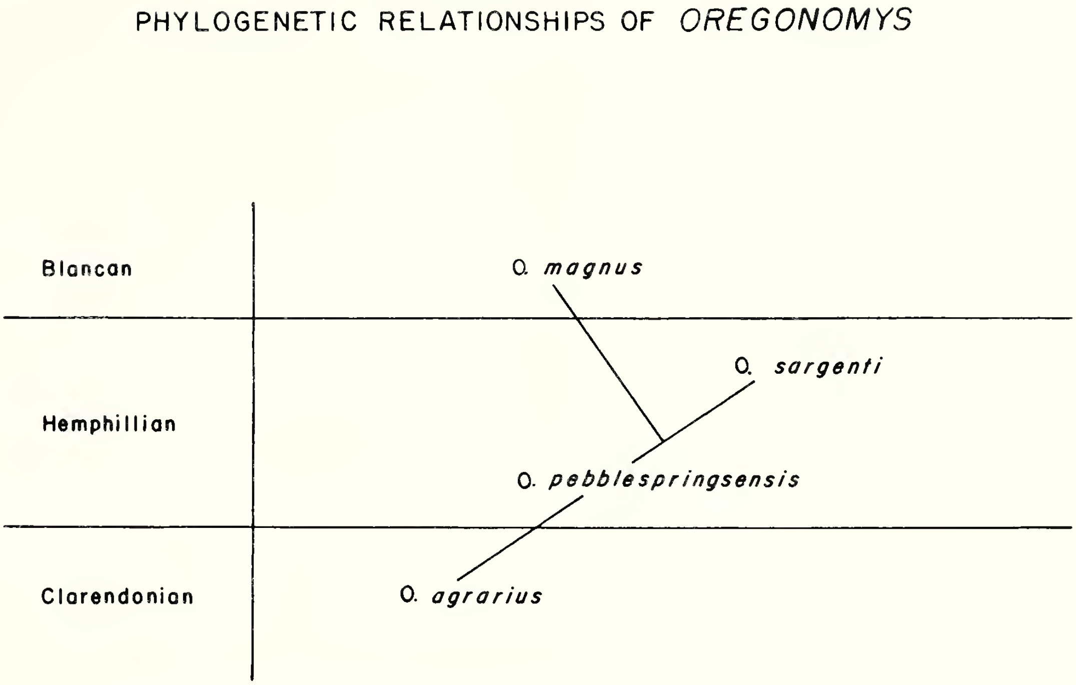

Fig. 16.—Possible phylogenetic relationships of some of the named species of *Oregonomys*.

large protocone which dominates the metaloph and partially fills the transverse valley. On the M^3 of *O. pebblespringsensis* and *O. sargenti*, the protocone is approximately the same size as the metacone. Therefore, the manner of loph union on the cheek teeth and the large protocone on M^3 distinguish *O. magnus* from the species from Oregon.

Until the discovery of SDSM 8749 (Fig. 14, g), the only known example of the lower dentition was UMMP V53563, a dentary with cheek teeth so worn that only lingual indentations remained on the occlusal surface. SDSM 8749 has little-worn teeth that display characteristics similar to those of the species from Oregon, such as a complex, multicuspid metalophid and a tricuspid protolophid on P_4. However, the anteroconid of *O. magnus* is a small crest rather than a distinct cusp, and there is no anterior cleft because the bicuspid anterior cingulid merges with the protoconid. A double connection of the lophids exists on the P_4 of *O. magnus* as in *O. sargenti*. However, the hypostylid is smaller and there is no angulation of the hypolophid on the molars, conditions more similar to that of *O. pebblespringsensis*. On SDSM 8749, the lophids of M_1–M_2 connect buccally like those of *O. pebblespringsensis*, but those of M_3 have a prominent medial connection. A feature that might indicate the greater hypsodonty of *O. magnus* compared with that of the other two species is the deeper valley between the anterior cingulid and the protoconid of M_1 on SDSM 8749. More specimens with less wear must be obtained before the validity of this feature can be substantiated. However, SDSM 8749 is distinctive in the construction of the metalophid of the P_4 and differs from *O. pebblespringsensis* in the manner of connection of the lophids on P_4 and M_3 and from *O. sargenti* in the morphology of the molars and the small hypostyle on P_4.

DISCUSSION

The morphology of these described species of *Oregonomys* suggests hypotheses pertaining to their habits and phylogeny. Wood (1935) described a portion of the skull and post-cranial skeleton of *O. agrarius*. On the basis of the small size of the occipitals, he concluded that the taxon had an expanded auditory region, and from the skeletal elements he deduced that *O. agrarius* had a richocetal or semi-richocetal locomotion (p. 196). The mastoids of *O. pebblespringsensis* are definitely inflated and the coronoid process of the dentary is deflected, perhaps indicating a species with similar habits. Therefore, two of the known species appear to parallel other pocket mice, such as *Dipodomys,* in morphology and, presumably, in habit. The cheek teeth of *O. sargenti* and *O. magnus* are similar to those of species of *Oregonomys* which possess modifications for saltation, suggesting closely related forms which may have had similar locomotor abilities. Comparison of the faunas in which these species occur with Recent faunas reinforces the supposition that *Oregonomys* is somewhat saltatorial. Geomyoids now living in the area consist of a geomyine (*Thomomys*), a perognathine (*Perognathus*), and *Dipodomys.* At Ordnance, Arlington, and McKay Reservoir, a geomyine, a perognathine, and *Oregonomys* existed. *Oregonomys* appears to have paralleled *Dipodomys,* which has more hypsodont cheek teeth and occupied a similar environmental position. Modern species of *Dipodomys* normally occur in semi-arid to arid environments. The great number of specimens of *Oregonomys* from Ordnance and Arlington, where castorids are rare, compared to the few known representatives from McKay Reservoir and Hagerman, where castorids are abundant, may indicate a drier environment at Ordnance and Arlington. Also, most of the known specimens of *O. sargenti* from McKay Reservoir were found in a coprolite, and so they might not have been locally derived. In conclusion, *Oregonomys* appears to have specializations parallel to those of *Dipodomys* and possibly was a member of a set of sympatric geomyoid species that resembles a set occurring today in the same region except for the absence in the fossil assemblage of a dipodomyine.

Certain dental structures suggest the phylogenetic relationships of the group (Fig. 16). The earliest known species, *O. agrarius,* from Clarendonian deposits near Ainsworth, Nebraska, has a simply constructed P_4 with only three cusps on the metalophid, and lower molars in which the lophs connect buccally. Then in the Hemphillian, a trend is seen in the succession from *O. pebblespringsensis* to *O. sargenti* toward acquistion of a molariform P_4 and medial union of the lophids of the cheek teeth. Unlike *O. agrarius, O. pebblespringsensis* has two or three cuspules on the anterior edge of the P_4. *O. sargenti* seems more advanced than *O. pebblespringsensis* because it has a crest-shaped cingulid on P_4 similar to that of the molars, a double connection of lophids on P_4 like the Blancan species, a continuous slope profile on the protoloph of P^4, perhaps indicating incipient hypsodonty, and medial connection of the lophids on the lower cheek teeth. The Blancan species, *O. magnus,* displays a medial union of lophs, even on M^1. However, this species does not appear to have come directly from *O. sargenti. O. magnus* retains some features found only in *O. pebblespringsensis,* such as lingual connection of the lophs of P^4, an abbreviated anterior profile of P^4, and a nonmolariform P_4. It shares with *O. sargenti* features such as double connection of the lophids on P_4 and the greater tendency for medial union of the lophs of the cheek teeth. Therefore, until more specimens of *O. magnus* can be obtained to define the limits of variation, it appears that the line from which *O. magnus* evolved diverged from *O. pebblespringsensis.*

LITERATURE CITED

Gazin, C. L. 1930. A Tertiary vertebrate fauna from the upper Cuyama drainage basin, California. Carnegie Inst. Washington Publ., 404:55–76.

Hibbard, C. W. 1939. Notes on additional fauna of Edson Quarry of the middle Pliocene of Kansas. Trans. Kansas Acad. Sci., 42:457–463.

———. 1941*a*. New mammals from the Rexroad fauna upper Pliocene of Kansas. Amer. Midl. Nat., 26:337–368.

———. 1941*b*. The Borchers fauna, a new Pleistocene interglacial fauna from Meade County, Kansas. Rpt. Studies, Kansas State Geol. Surv. Bull., 38:197–220.

———. 1949. Pliocene Saw Rock Canyon fauna in Kansas. Contr. Mus. Paleont., Univ. Michigan, 7:91–105.

———. 1950. Mammals of the Rexroad Formation from Fox Canyon, Meade County, Kansas. Contr. Mus. Paleont., Univ. Michigan, 8:113–192.

Hutchison, J. H. 1968. Fossil Talpidae (Insectivora, Mammalia) from the later Tertiary of Oregon. Bull. Mus. Nat. Hist., Univ. Oregon, 11:1–117.

Jacobs, L. L. 1977. Rodents of the Hemphillian age Redington local fauna, San Pedro Valley, Arizona. J. Paleont., 51:505–519.

James, G. T. 1963. Paleontology and nonmarine stratigraphy of the Cuyama Valley badlands, California. Part 1. Geology, faunal interpretations, and systematic descriptions of Chiroptera, Insectivora, and Rodentia. Univ. California Publ. Geol. Sci., 45:1–171 pp.

Kellogg, L. 1910. Rodent fauna of the late Tertiary beds at Virgin Valley and Thousand Creek, Nevada. Univ. California Publ. Geol. Sci., 5:421–437.

Korth, W. W. 1979. Geomyoid rodents from the Valentine Formation of Knox County, Nebraska. Ann. Carnegie Mus., 48:287–310.

Newcomb, R. C. 1966. Lithology and eastward extension of the

Dalles Formation, Oregon and Washington. U.S. Geol. Surv. Prof. Pap., 550D:D59–D63.

———. 1971. Relation of the Ellensburg Formation to extensions of the Dalles Formation in the area of Arlington and Shutler Flat, north central Oregon. OreBin, 33:133–142.

Rensberger, J. M. 1971. Entoptychine pocket gophers (Mammalia, Geomyoidea) of the early Miocene John Day Formation, Oregon. Univ. California Publ. Geol. Sci., 90:1–209.

Shotwell, J. A. 1956. Hemphillian mammalian assemblage from northeastern Oregon. Bull. Geol. Soc. Amer., 67:717–738.

———. 1958. Inter-community relationships in Hemphillian (mid-Pliocene) mammals. Ecology, 39:271–282.

———. 1967. Late Tertiary geomyoid rodents of Oregon. Bull. Mus. Nat. Hist., Univ. Oregon, 9:1–51.

———. 1970. Pliocene mammals of southeastern Oregon and adjacent Idaho. Bull. Mus. Nat. Hist., Univ. Oregon, 17:1–103.

Storer, J. E. 1970. New rodents and lagomorphs from the upper Miocene Wood Mountain Formation of southern Saskatchewan. Canadian J. Earth Sci., 7:1125–1129.

———. 1975. Tertiary mammals of Saskatchewan. Part III. The Miocene fauna. Life Sci. Contr., Royal Ontario Mus., 103:1–134.

Wilson, R. W. 1937. Pliocene rodents of western North America. Carnegie Inst. Washington Publ. 487:21–73.

Wood, A. E. 1935. Evolution and relationships of the heteromyid rodents with new forms from the Tertiary of western North America. Ann. Carnegie Mus., 24:73–262.

Zakrzewski, R. J. 1969. The rodents from the Hagerman local fauna, upper Pliocene of Idaho. Contr. Mus. Paleont., Univ. Michigan, 23:1–36.

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REVISION OF THE FOSSIL AND RECENT LEMMINAE (RODENTIA, MAMMALIA)

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ABSTRACT

The fossil history of the Lemminae is revised and three genera are recognized: *Lemmus* with *Myopus* as a subgenus; *Synaptomys* with the subgenus *Plioctomys*; and *Mictomys*, which contains two additional subgenera, *Metaxyomys* and *Kentuckomys* (new). *Dicrostonyx* and *Lagurus* are excluded from the Lemminae. The Lemminae are thought to have originated in Eurasia and the bog lemmings Synaptomyini immigrated to North America in the late Pliocene (Blancan).

ZUSAMMENFASSUNG

Die Stammesgeschichte der Lemminae wird revidiert. Dazu gehören drei Gattungen, jeweils mit mehreren Untergattungen: *Lemmus* mit *Lemmus* und *Myopus*, *Synaptomys* mit *Synaptomys* und *Plioctomys*, *Mictomys* mit *Mictomys*, *Metaxyomys*, und mit der neuen Untergattung *Kentuckomys*. Nicht zu den Lemminae gehören die Gattungen *Dicrostonyx* und *Lagurus*. Es wird angenommen, dass die Lemminae ihren Ursprung in Eurasien haben, von wo die "bog lemmings" Synaptomyini im späten Pliozän (Blancan) nach Nordamerika gelangt sind.

INTRODUCTION

R. W. Wilson (1933) was the first person to describe a valid taxon of extinct lemming when he described *Synaptomys vetus*. His work on fossil arvicolids (Wilson, 1932, 1933, 1937) laid the groundwork for C. W. Hibbard and all other later workers on the North American radiation of these interesting and important animals. It is especially appropriate that a volume in Professor Wilson's honor should include a revision of the fossil and recent Lemminae.

Lemmings form a distinct group within the Arvicolidae, and they were among the first arvicolids to develop rootless molars with high dentine tracts. However, the common term "lemming" includes several independent groups of arctic to cool-temperate small rodents. The central genus is *Lemmus* and we regard it and its close relatives as constituting the subfamily Lemminae (Gray, 1825). This subfamily contains three genera: *Lemmus, Synaptomys* and *Mictomys*, all of which contain two or more subgenera. The genera are still extant but several of the subgenera are extinct.

The stratigraphic sequence of fossil lemmings in this paper is tied into a system (Fig. 1) of North American Arvicolid Zones (NAAZ) proposed by Martin (1979). The earliest Lemminae are described from the Villafranchian of Russia as *Synaptomys* (*Plioctomys*) (Suchov, 1966). In North America the Lemminae appear in the upper part of NAAZ II (late Rexroadian) or in NAAZ III (Senecan, see Schultz et al., 1978).

We do not regard the gray lemmings (Lagurinae) of Eurasia and North America as true lemmings, as they lack the lemming enamel structure (Koenigswald, 1980). The Dicrostonychinae (Chaline, 1972) have short lower incisors and an arctic distribution as do the Lemminae, but they differ from the subfamily in molar enamel structure (Koenigswald, 1980) and in caecum and karyotype (Rausch, 1978). Well defined members of the Lemminae are present in Blancan and Villafranchian faunas in North America and Europe, and any postulated relationship with collared lemmings must predate that time and would therefore date from a very basal portion of the arvicolid radiation. Besides these other arguments the Dicrostonychinae show evolutionary trends, including a progressive increase in alternating triangles (Guthrie and Matthews, 1971; Agadjanian and Koenigswald, 1977), which contrast with the condition in the Lemminae. The only character which might unite the two subfamilies is the short lower incisors, a condition which has been regarded as resulting from convergence (Kowalski, 1977).

The subfamily Lemminae may be characterized by a simple dental pattern of three alternating triangles on M_1 coupled with evergrowing molars, cementum, and high dentine tracts. The upper incisors bear a shallow lateral groove (found in some indi-

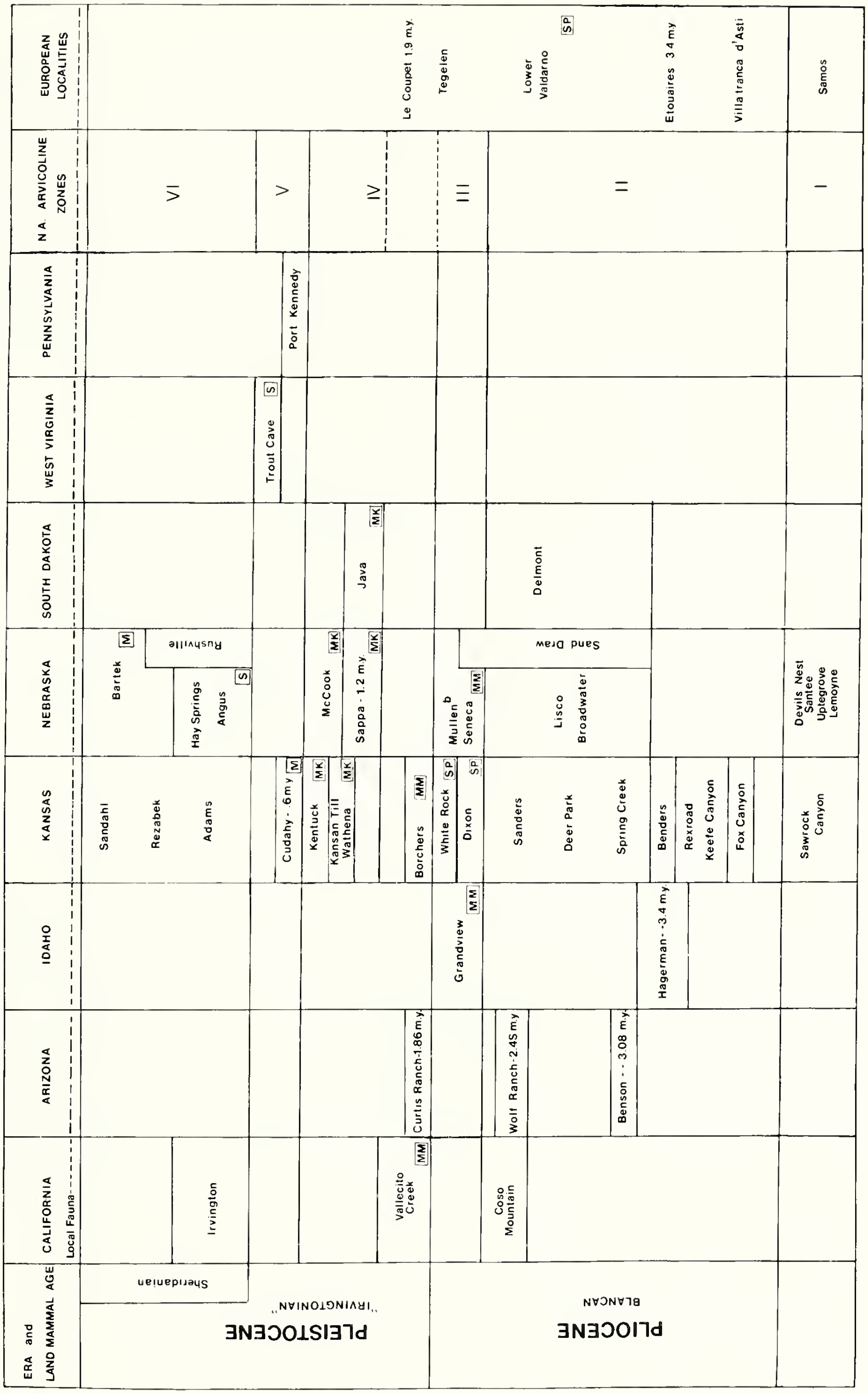

Fig. 1.—Relationships (modified from Martin, 1979) of selected faunas to the North American Arvicolid Zones (NAAZ) and the stratigraphic distribution of bog lemmings prior to the Rancholabrean. SP = *Synaptomys* (*Plioctomys*); S = *Synaptomys* (*Synaptomys*); MM = *Mictomys* (*Metaxyomys*); MK = *Mictomys* (*Kentuckomys*); M = *Mictomys* (*Mictomys*).

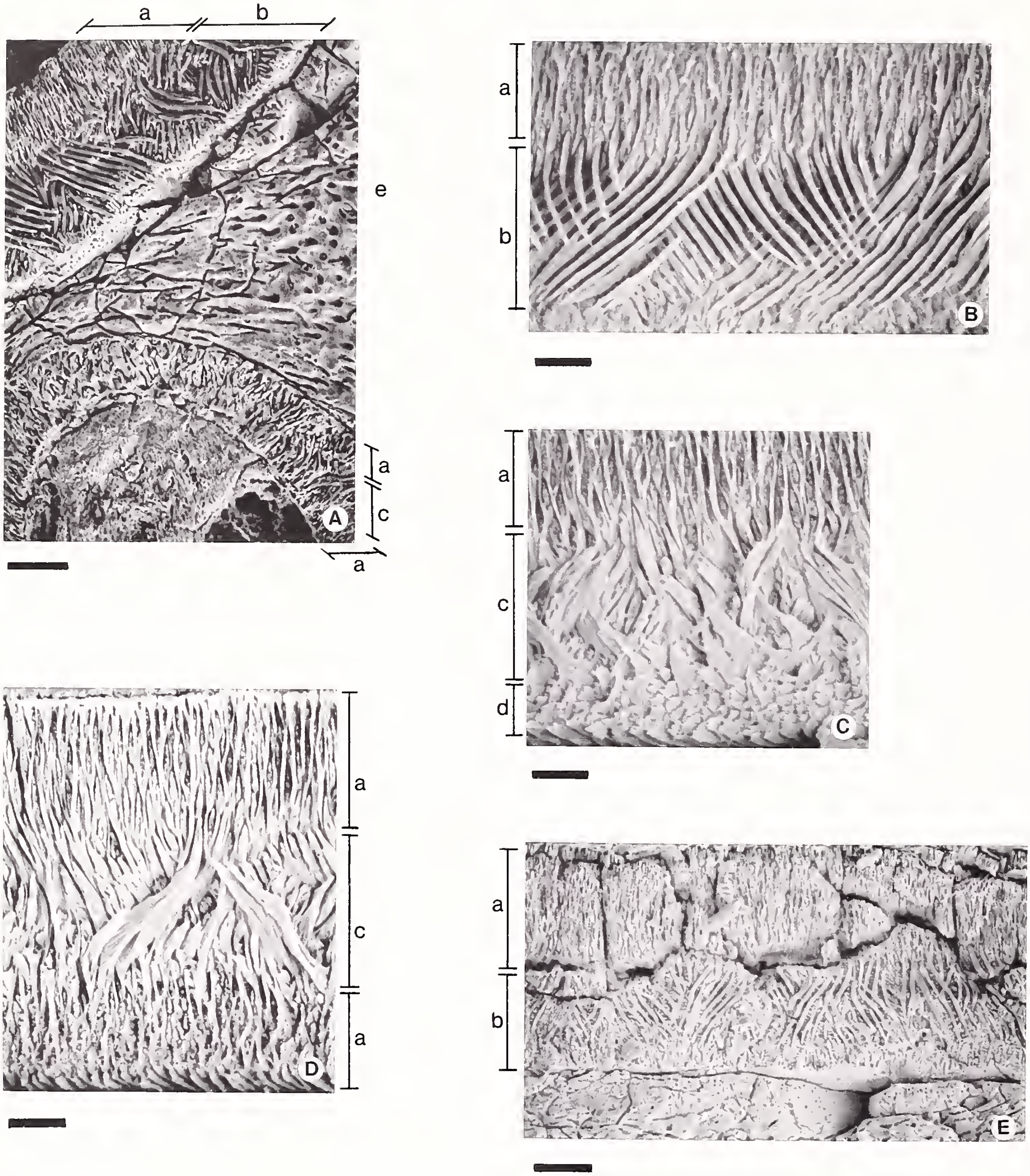

Fig. 2.—Scanning electron microscope (SEM) photographs of cross-sections of the enamel structure (Schmelzmuster) of lemming molars taken parallel to the chewing surface. A. *Mictomys* (*Metaxyomys*) *vetus* showing the leading edge (top of the photograph) and trailing edge with reduced enamel thickness at the apex of the syncline (bottom of the photograph). B–D. *Lemmus sibiricus*. B. Leading edge, C–D. Trailing edges showing three layer structure. E. *Mictomys* (*Metaxyomys*) *vetus* leading edge showing the fractures in the radial enamel caused by grinding stopping at the junction with the lamellar enamel. a. radial enamel, b. lamellar enamel, c. lemming enamel, d. tangential enamel, e. dentine. Bar = .2 mm in A and .1 in B–E.

viduals of all forms, *contra* Howell [1927] who restricted this character to *Synaptomys*). The trailing edges (see below) of the triangles on the molars contain a special enamel structure described by Koenigswald (1980) as "less symmetrical lamellar enamel," but here called lemming enamel.

General trends within the phylogeny of the Lemminae include the following:

1. The longitudinal tooth axis shifts towards the labial side in the lower molars and towards the lingual side in the upper molars. This shift does not extend as far in any upper molars as it does in the lower molars of some subgenera.

2. The lower incisors become shorter in some lineages.

3. The enamel on the trailing edges of the alternating triangles and the posterior loop becomes thinner by reduction of the outer layer, and, in progressive forms, the second enamel layer also. This thinning begins in the apex of the synclines (Fig. 2, A).

The polarity of these trends is supported by outgroup comparisons with other arvicolids and cricetids, functional trends, and the stratigraphic distribution of the characters involved. We would not expect reversals within these trends, but parallel evolution is not unlikely.

MATERIALS AND METHODS

We have been able to study the type or topotypical material of the following fossil taxa: *Synaptomys europaeus, S. rinkeri, S. bunkeri, Mictomys vetus, M. kansasensis,* and *M. meltoni.* We have studied referred material of *M.* cf. *vetus* from the Seneca Local Fauna, *M. kansasensis* from the McCook, Wathena, and Sappa Local Faunas, and *Synpatomys cooperi* from the Trout Cave Local Fauna. We have also studied Subrecent or Recent material of *Lemmus sibiricus* from Banks Island, Canada; *Myopus schisticolor* from Sweden; *Synaptomys cooperi* from Kansas; and *Mictomys borealis* from the Gaspé Peninsula, Canada, and Alaska.

Molars of lemmings selected for enamel investigation were imbedded in an artificial resin and ground down parallel to the chewing surface until the enamel band was visible for its whole length. The polished surfaces were then etched for 2–3 seconds in 2 N hydrochloric acid. After sputtercoating the enamel structure was examined with the aid of a scanning electron microscope at magnifications of from 600–1,250 ×.

Koenigswald (1977, 1980) has shown that the enamel in arvicolid molars is composed of different types, which are defined by the orientation of the enamel prisms. The three basic types are:

1. *Radial Enamel.* This enamel type is regarded as primitive for the group. Prisms rise against the outer surface of the enamel while interprismatic substance (oriented radially) crosses the prisms at about a right angle. In the drawings, areas with this enamel are left white (Fig. 2, B).

2. *Tangential Enamel.* The relation of prisms and interprismatic substance is the same as in radial enamel, but the prisms lie more or less parallel to the chewing surface, as does the interprismatic substance. The prisms point laterally. Tangential enamel is derived from radial enamel by turning the whole enamel structure by about 90°. Primitive tangential enamel is defined as the intermediate condition where the prisms are bent at an angle of about 45° (Fig. 2, C).

3. *Lamellar Enamel.* In this type, single layers of prisms form lamellae nearly parallel to the chewing surface. Within a lamella all prisms are parallel, but they form an angle of about 90° with the prisms of the underlying and overlying lamellae. The interprismatic substance strengthens the enamel in the third dimension. In earlier stages of evolution lamellae penetrate the chewing surface at steeper angles and are more difficult to identify (Fig. 2, B).

A fourth type of enamel derived from radial enamel may be distinguished in the Lemminae and we therefore call it "lemming enamel." In this type the lamellae "move" up and down in the section and are not parallel to the chewing surface. Their lateral extension is much shorter than in typical lamellar enamel, although lemming enamel usually continues laterally into typical lamellar enamel (Fig. 2, B).

The arrangement of these different enamel types within any given chewing surface is called its "Schmelzmuster" (Koenigswald, 1980). It is to be distinguished from the term "enamel pattern" which is used for the arrangement of the dentine triangles. The Schmelzmuster is repeated from one dentine triangle to the next, but the anterior and posterior sides of the triangles show different arrangements of enamel types (Fig. 2, A). As a result of the propalinal movement of the jaw during mastication the anterior cutting edges of the lower triangles and the posterior cutting edges of the upper triangles occlude first and are thus referred to here as "leading edges." The posterior cutting edges of the triangles of the lower molars and the anterior edges of the upper molars are called "trailing edges." These terms were introduced by Greaves (1973) and are very useful in understanding the functional morphology of teeth. All leading edges in both upper and lower molars share the same Schmelzmuster, while all trailing edges share a different one. In the special case of a severe shift in the longitudinal tooth axis, such as occurs in some lemmings, the reduced triangles may differ somewhat from the enlarged ones. There is some variation along the enamel band in any tooth and in most of the taxa described in this paper the description of a typical leading edge and trailing edge is based on the examination of several molars whose entire enamel surface was scanned. All photos and drawings are oriented so that the directions of chewing forces during mastication meet the enamel band from the top of the figure. Thus upper molars are figured upside down from conventional orientations.

The functional significance of the different arrangements of apatite prisms in the enamel of arvicolid molars seems to be related to the direction of chewing forces (Koenigswald, 1980). The primitive arrangement for arvicolids (the only type found in most of the early members of the arvicolid radiation and in some cricetids) is radial enamel. This arrangement when stressed by the directional forces of chewing permits fractures readily to transect the entire thickness of the enamel. Arvicolids with only radial enamel usually compensate for this by having very thick enamel. Lamellar or tangential enamel inhibit fractures from passing through the enamel (see Fig. 2, E) and thereby preserve the enamel edges, extending the lifespan of the tooth.

Another trend whose functional significance has been discussed by Koenigswald (1980) is the thinning of the enamel bands. This is permitted in part by the greater structural strength of the derived Schmelzmusters. However, it appears to be advantageous to retain some radial enamel in the Schmelzmuster. The radial enamel is more resistant to abrasion than the lamellar enamel is, but it is more vulnerable to cracks. The lamellar enamel is more elastic, and the cutting edge is maintained by radial enamel underlain by a cushion of lamellar enamel (Koenigswald, 1980: 86).

SYSTEMATIC ACCOUNTS

Order Rodentia
Family Arvicolidae
Subfamily Lemminae
Tribe Lemmini

Genus **Lemmus** Link, 1795

Diagnostic dental characters.—Lingual and labial triangles in M_1 of about equal size so that there is no shift of the longitudinal tooth axis; anterior loop of M_1 pointed; first lingual and second labial reentrants (terminology as in Koenigswald, 1980, fig. 1) opposite each other on M^3 (Fig. 7); trailing edges of the enamel bands on the molars consisting of three layers.

Subgenus **Lemmus**

Material examined for Schmelzmuster.—*Lemmus sibiricus*, M_1, Recent, from Banks Island, NWT, Canada; *Lemmus lemmus*, several M_1's from the Upper Pleistocene of Germany.

Comments.—The species of *Lemmus* differ mainly in pelage and not in dental characters. According to the latest review of European lemmings (Kowalski, 1977) the genus *Lemmus* has occurred there since the late Middle Villafranchian (Tegelian). This material is regarded as belonging to *Lemmus lemmus*. Several localities in Germany, France, Hungary, Poland and Roumania have produced fossil *Lemmus* throughout the Pleistocene (Terzea, 1972). In the Lower and Middle Pleistocene, references for *Lemmus* may also include *Myopus*. In the Upper Pleistocene, *Lemmus* in Central Europe is taken to be characteristic of glacial periods. In the Middle Pleistocene (NAAZ V) Cape Deceit Fauna of Alaska (Guthrie and Matthews, 1971) we find *Lemmus sibiricus*. This is the earliest record of *Lemmus* in North America. The Schmelzmuster of *Lemmus* is differentiated into leading and trailing edges. The leading edge is built from an inner layer of lamellar enamel and an outer one of radial enamel (Fig. 2, B). The trailing edge consists of three layers (Fig. 2, C, D; Fig. 4, A): an inner one of radial enamel which rotates into a band of lemming enamel, the lemming enamel is then overlain by a shield layer containing radial (Fig. 2, D) or in some parts tangential enamel (Fig. 2, C). *Lemmus* is the least derived lemming dentally but its Schmelzmuster is fully developed and the history of its origin cannot now be traced in the fossil record.

Subgenus **Myopus** Miller, 1910

Material examined for Schmelzmuster.—M_1 and M_2 of *Myopus schisticolor* from Sweden.

Diagnostic dental characters.—None except size. The description of *Lemmus lemmus* also applies here.

Comments.—*Myopus* differs from *Lemmus* in characters of the manus (Miller, 1912:610) but these characters cannot be verified in the known fossil material and no differences were noted between the Schmelzmuster of *Lemmus* and *Myopus*.

In the Middle Pleistocene of Europe (Arvicola-Zone 1 of Koenigswald, 1973) a small member of the Lemminae occurs with *Lemmus*. Kowalski (1977:306) has shown that the length of M_1 in *Lemmus* stays constant over a very great length of time, and the smaller lemming may be assumed to represent an early *Myopus schisticolor*. Kowalski (1977: 302) regarded these smaller teeth as those of younger animals, but his interpretation is unlikely since the mean of the length of all M_1's in localities like Tarkö or Petersbuch is distinctly smaller than in *Lemmus* (*Lemmus*).

Tribe Synaptomyini

Diagnostic dental characters.—Lemmings with the first lingual and second labial reentrant angles alternating on M^3, and the longitudinal tooth axis shifted on the molars.

Genus **Synaptomys**

Diagnostic dental characters.—Lemmings with the first and second alternating triangles on the lower molars not broadly confluent.

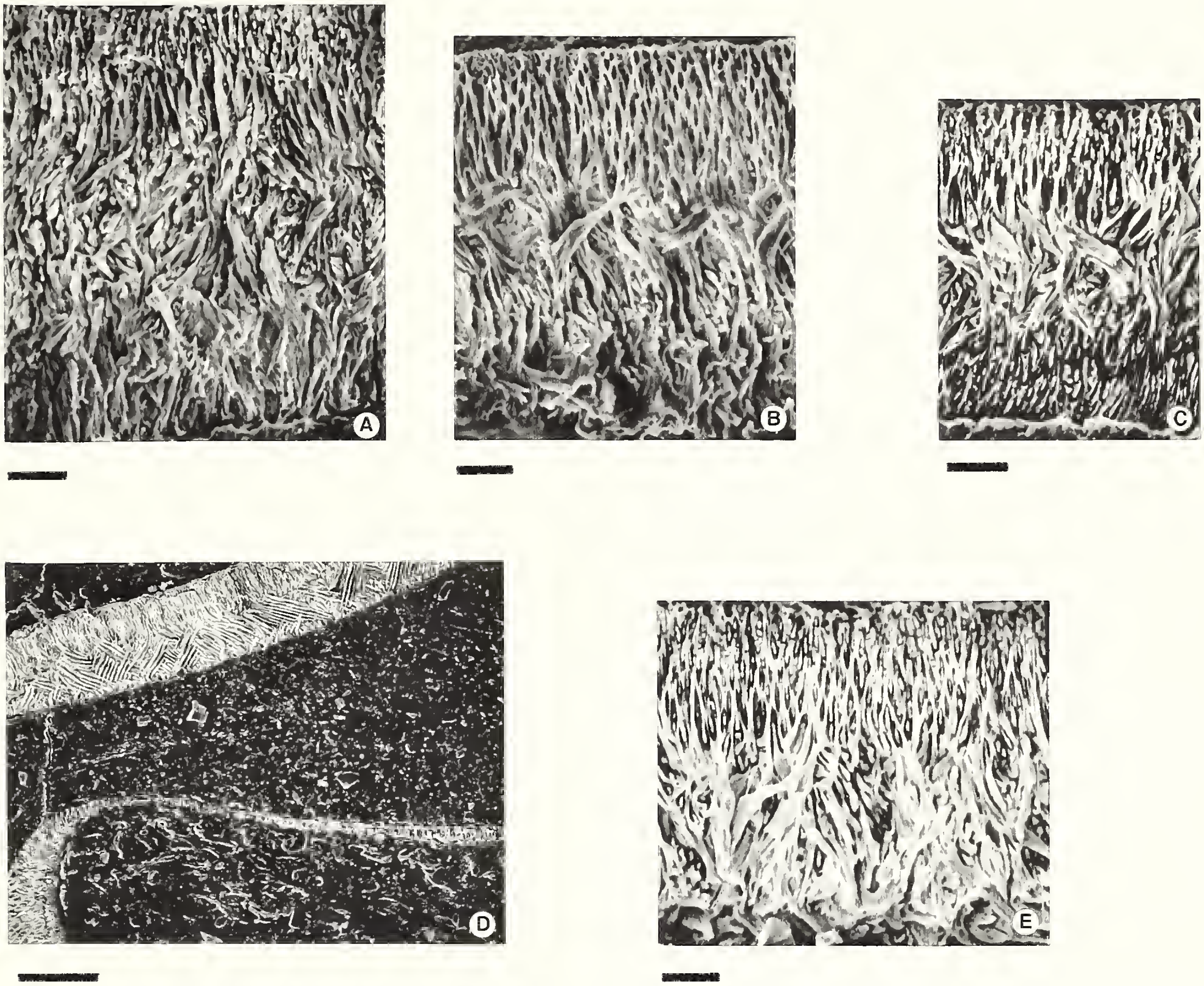

Fig. 3.—SEM photographs of cross-sections of *Synaptomys* molar enamel taken parallel to the chewing surface. A–C, trailing edges showing the typical three-layered Schmelzmuster, A. *S.* (*Plioctomys*) *rinkeri,* B. *S.* (*Plioctomys*) *europaeus,* C. *S.* (*Synaptomys*) *cooperi,* D. *S.* (*Synaptomys*) *cooperi* with leading edge at top of photograph and trailing edge at the bottom, notice the extreme thinning to radial enamel near the apex of the syncline. E. Typical trailing edge enamel *S.* (*Synaptomys*) *cooperi* showing an inner layer of radial enamel and an outer layer of lemming enamel. Bar = .1 mm in A, B, C, and E. Bar = .5 mm in D.

Subgenus *Synaptomys* Baird, 1857

Diagnostic dental characters.—Lemmings with the longitudinal axis of the molars shifted more than in *Plioctomys* and the enamel of the trailing edges of the alternating triangles and the posterior loop reduced to two layers.

Synaptomys* (*Synaptomys*) *cooperi Baird, 1857

Material examined for Schmelzmuster.—Right M_1 and left M_1 from Trout Cave in West Virginia (NAAZ V) and a Recent right M_1 from Atchinson County, Kansas.

Description of the Schmelzmuster.—The enamel of the trailing edges in the molars of *S. cooperi* is characterized by Schmelzmuster (Fig. 4, D) reduction, leaving an outer layer of lemming enamel (about 50% of the thickness) and an inner layer of radial enamel (Fig. 3, E). As the enamel shrinks to about 5 μ in thickness towards the inner corner of the syncline (Fig. 3, D), the lemming enamel disappears leaving only the inner radial enamel. On the other hand, the outer edge of the syncline (on the trailing edge) near the dentine tract is thick (about 50 μ) and composed of three layers as in *Lemmus* (Fig. 3, C). In the material from Trout Cave (NAAZ V) the amount of extremely thinned enamel seems to be less than in the Recent material.

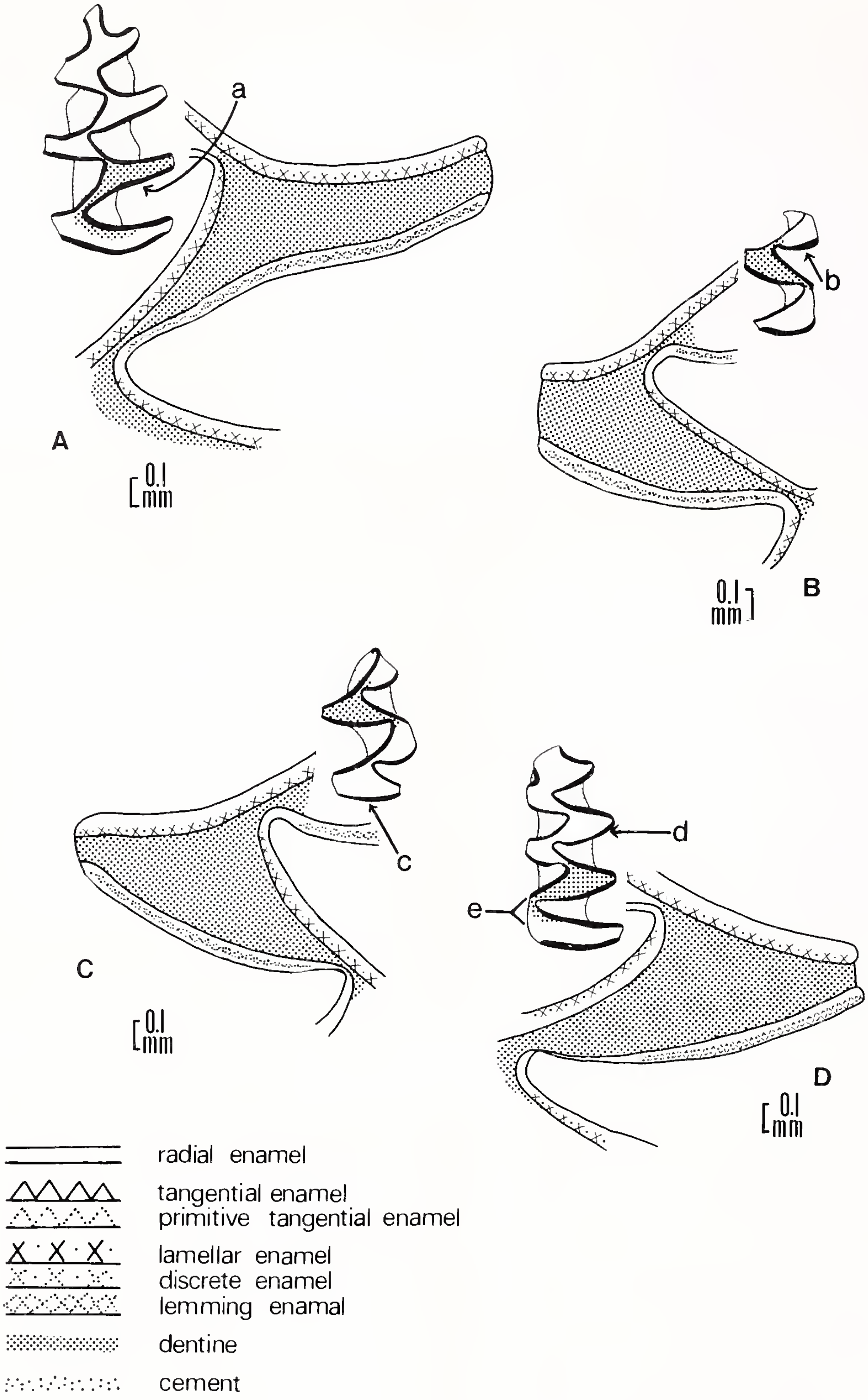

Fig. 4.—Schematic drawings of Schmelzmusters. A. *Lemmus sibiricus*, left M_1, from Banks Island, Canadian Arctic (a = location of Fig. 2, D). B. *S.* (*Plioctomys*) *europaeus*, left M^2 from Rebielice, Poland (b = location of Fig. 3, B). C. *S.* (*P.*) *rinkeri*, left M^1, UMMP 32070, paratype, (c = location of Fig. 3, A). D. *S.* (*Synaptomys*) *cooperi*, left M_1 from Kansas (d = location of Fig. 3, E; e = location of Fig. 3, D).

Discussion.—The earliest record of *Synaptomys* (*Synaptomys*) appears to be material of *S. cooperi* from Trout Cave. On the basis of other arvicolids this locality should fall (at least in its lower part) into NAAZ V making it roughly contemporaneous with the Cudahy faunas in western Kansas. Examination of enamel from the Trout Cave *Synaptomys* reveals that it already has the reduction of the trailing edge to two layers found in *S. cooperi.* The next oldest *cooperi* we have is from the Angus Local Fauna in southcentral Nebraska (NAAZ VI) where we have a population of small individuals. Two extinct species, *S. australis* and *S. bunkeri,* have been described for the relatively large forms found in southern localities (Florida and Meade County, Kansas). Those forms are mostly from NAAZ VII (Rancholabrean), and we have not attempted to review their specific status, although there seems to be little chance that *S. bunkeri* is valid.

Subgenus **Plioctomys** Suchov, 1976

Diagnostic dental characters.—Lemmings with the typical three-layered enamel on the trailing edges of the triangles as is found in *Lemmus,* but differing from that genus in having the longitudinal tooth axis slightly shifted labially on the lower molars and lingually on the upper molars; posterior loop of M^3 small and rounded.

Synaptomys* (*Plioctomys*) *europaeus Kowalski 1972

Material examined for Schmelzmuster.—M^2 from Rebielice Krolewskie II, Poland.

Description of the Schmelzmuster.—The leading edges of the triangles are like those in *Lemmus* and the trailing edges have three layers as in that genus (Fig. 3, B; Fig. 4, B). The lemming enamel lies between inner and outer layers of radial enamel and the prisms in the outer layer tend to incline forming tangential enamel. There are fewer lamellae per unit area in the lemming enamel of this form than there are in the lemming enamel of *Lemmus.*

Discussion.—O. Fejfar drew our attention to *Synaptomys* (*Plioctomys*) *mimomiformis* which was described in Suchov (1976) from the Csarnotanum of Russia. This is the oldest known lemming and judging from the figures (Suchov, 1976, fig. 1) it is very similar to the next oldest lemming, *Synaptomys* (*Praesynaptomys*) *europaeus.* We regard *Praesynaptomys* as a junior synonym of *Plioctomys,* but we do not believe that they should be considered conspecific without more direct comparisons than we are able to make.

Synaptomys* (*Plioctomys*) *rinkeri Hibbard, 1956

Material examined for Schmelzmuster.—Left M^1, UMMP 32070, paratype.

Description of the Schmelzmuster.—The leading edges of the triangles have enamel about 76 μ thick, and more than 50% of this thickness is in the lamellar enamel which forms the inner layer. The outer layer is radial enamel. The trailing edges of the triangles consist of three layers (Fig. 3, A; Fig. 4, C): an inner radial enamel which composes about 20% of the thickness, a middle layer of lemming enamel which makes up about 50% and an outer layer of radial to tangential enamel which makes up about 30% of the thickness. The trailing edges appear to be nearly as thick as the leading edges on the triangles (around 70 μ). The closing enamel of the posterior loop shows the same structure as the trailing edges of the triangles but it is about 80 μ thick.

Discussion.—This is probably the oldest lemming in North America. The muskrat from this locality was referred to as *Pliopotamys meadensis* by Hibbard (1956) suggesting an age of NAAZ II, but Eshelman (1975) reports cement in the reentrant angles of these muskrat molars, which suggests *Ondatra* rather than *Pliopotamys.* On this basis Martin (1979) placed the Dixon Local Fauna in NAAZ III. It may, however, be somewhat older than the Grandview or Seneca Local Faunas which contain the earliest records of *Metaxyomys. Synaptomys* cf. *rinkeri* is reported by Eshelman (1975) from the White Rock Local Fauna. Although we have not examined this material, we would tentatively assign it to *Plioctomys* on the basis of Eshelman's species identification. In this case, *Plioctomys* is clearly associated with arvicolines (*Ondatra idahoensis*; *Pliophenacomys osborni*) characteristic of NAAZ III. The Dixon Local Fauna is at the very base of this zone and enough time may exist for a separation of *Synaptomys* and *Metaxyomys* lines within that zone. Alternatively, *Plioctomys* might have arrived in North America in the top of NAAZ II thus providing an almost simultaneous appearance in North America and Europe.

In *Synaptomys* (*Plioctomys*) the anterior loop on M_1 tends to be more elongate (*Lemmus*-like) than in *S.* (*Synaptomys*) and all three enamel layers are present on the trailing edges of the alternating triangles [enamel reduced in *S.* (*Synaptomys*)]. *Synaptomys* (*Plioctomys*) *rinkeri* differs from *S.* (*P.*) *europaeus* in having more reduction of the labial triangles in relationship to the lingual ones in the lower molars. *S.* (*P.*) *europaeus* differs little from *Lemmus* in this respect.

Synaptomys (*Plioctomys*) *rinkeri* must stand close to the common stem from which all other North American bog lemmings were derived. It is in all known respects more primitive than other North American Lemminae.

Genus ***Mictomys*** True, 1894

Diagnostic dental characters.—Lower molars with first and second alternating triangles broadly confluent, because of flattening of the first external reentrant fold.

Subgenus ***Mictomys*** True, 1894

Diagnostic dental characters.—Lemmings with the tooth axis of the lower molars shifted to the labial side and the trailing edges of the molars reduced to a Schmelzmuster of two layers; lower incisors terminating posteriorly anterior to M_3.

Mictomys* (*Mictomys*) *borealis

Diagnostic dental characters.—Enamel of the trailing edges of the molars reduced to radial and lemming enamel layers; incisor terminating near the anterior edge of M_3; no labial cement on the lower molars.

Material examined for Schmelzmuster.—Left M_1 from Fairbanks, Alaska.

Description of the Schmelzmuster.—The leading edges of the lower molars of *Mictomys borealis* are about 50 μ thick, and about half this thickness is lamellar enamel on the inner side of the enamel band. The trailing edge is thinner (around 40 μ) and is continuously two layered with an inner layer of radial enamel and an outer layer of lemming enamel. The closing enamel in the posterior loop shows the same arrangement. The shallow reentrant folds on the labial side do not have the Schmelzmuster differentiated between the trailing and leading edges except in the first triangle. The second and third triangles show a continuous layer of lamellar enamel in the inner half of the enamel band and radial enamel on the outer.

Mictomys* (*Mictomys*) *meltoni Paulson, 1961

Diagnostic dental characters.—Enamel somewhat more differentiated than in *M. borealis*; teeth larger than in that species; first triangle on the lower molars with a convex border (Paulson, 1961).

Material examined for Schmelzmuster.—Right M_1, left M_3, and a left M^2 from the type locality (KUVP Coll. Loc. Meade Co. 10, NAAZ V).

Description of the Schmelzmuster.—The four major lingual triangles of the lower molars have leading edges about 60 μ thick and they are composed of two layers of about equal thickness. The inner layer is lamellar enamel and the outer layer, which may be somewhat thinner, is radial enamel. The trailing edge is thinned to about 35 μ but also consists of two layers, an inner layer of radial enamel and an outer layer of lemming enamel.

On the labial side of the lower molars the triangles are strongly reduced with only shallow synclines left between them. The first and second synclines have differentiated enamel according to trailing and leading edges as on the lingual side, but the third syncline has lamellar enamel inside of radial enamel on both trailing and leading edges.

Discussion.—Paulson (1961) and Semken (1966) have argued that *M. meltoni* cannot be ancestral to *M. borealis* because it has less enamel reduction, equal enamel thickness on the trailing and leading edges of the triangles, and a cement filled first labial reentrant angle on M_3. The reduction of enamel and the presence or absence of cement is somewhat variable in the teeth we examined. The observation that the enamel is of equal thickness on front and back edges of triangles in *M. borealis* seems to be a persistent error, because the specimens we examined showed some reduction in the thickness of trailing edges and the enamel itself is reduced to two layers. *M.* (*Mictomys*) *meltoni* occurs in faunas belonging to NAAZ V in Meade County, Kansas. The type material is from University of Kansas Vertebrate Paleontology collecting locality (KUVP) Meade County 10, and is from the Atwater Member of the Crooked Creek Formation.

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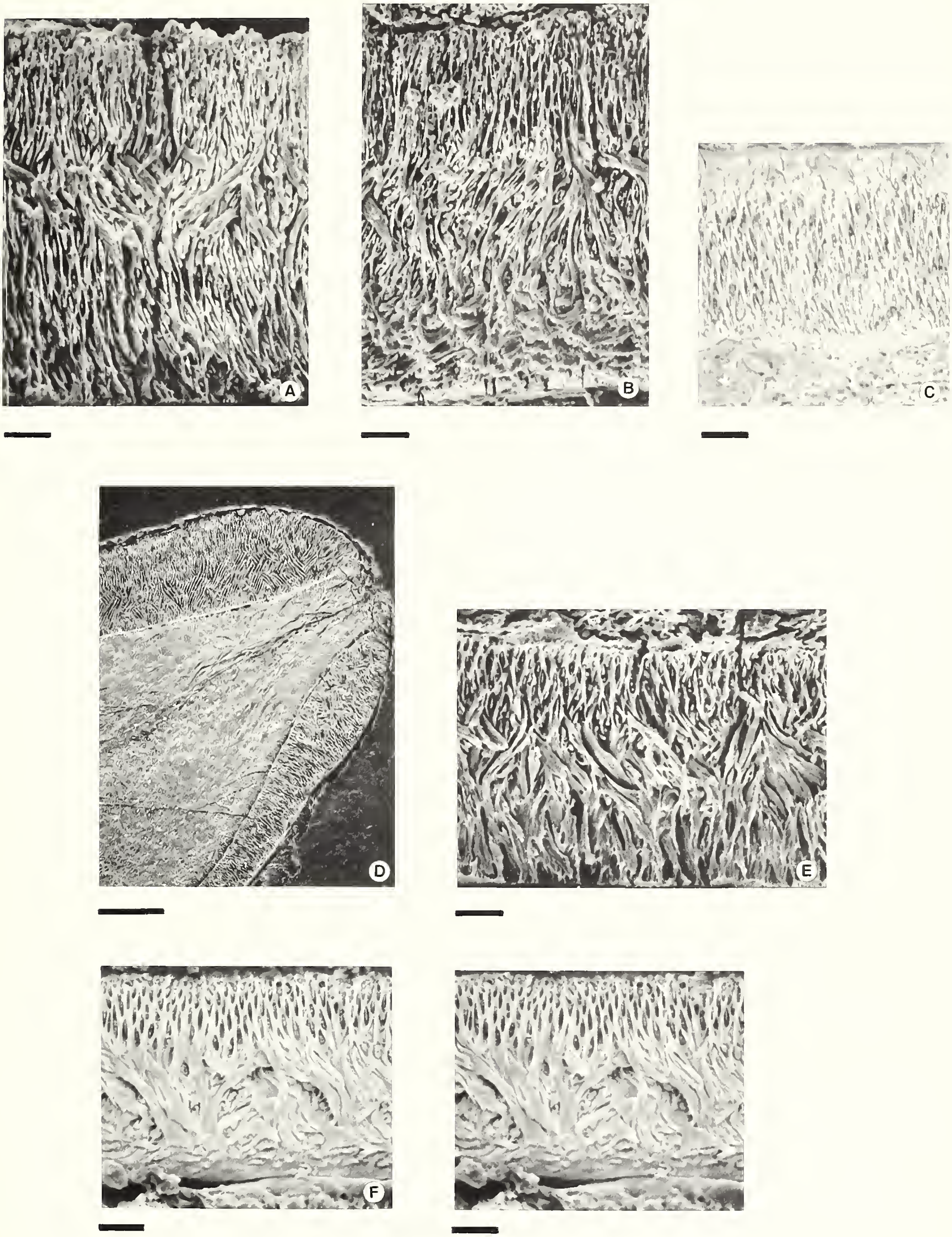
Fig. 5.—SEM photographs of cross-sections of *Mictomys* molar enamel taken parallel to the chewing surface. A–B. *M.* (*Metaxyomys*) showing typical three-layered trailing edges. A. *M.* (*Metaxyomys*) *vetus*. B. *M. Metaxyomys landesi*. C–E. *M.* (*Kentuckomys*) *kansasensis*. C. Typical trailing edge showing reduction to radial enamel. D. Apex of an anticline showing leading edge (top) and a trailing edge with a cushion of three-layered enamel blending into a single layer of radial enamel. E. Closing enamel of M^1 showing lemming enamel and radial enamel. F. Stereophotograph of two-layered trailing edge enamel in *M.* (*Mictomys*) *borealis* from the Gaspé Peninsula. Bar = .1 mm in A, B, C, E, F, and G. Bar = .5 mm in D.


A
B
C
D
E
F

Subgenus *Metaxyomys* Zakrzewski, 1972

Diagnostic dental characters.—Trailing edges of the alternating triangles with the primitive three-layered Schmelzmuster; the tooth axis not shifted as much as in *Mictomys* (*Mictomys*); capsular process for the lower incisor more anterior than in *Synaptomys.*

Mictomys (*Metaxyomys*) *vetus* (Wilson, 1933)

Material examined.—Topotypical jaws and teeth were examined but no enamel sections were made. The description of the Schmelzmuster is based on tentatively referred material from the Seneca Local Fauna (NAAZ III) of Nebraska. This material is smaller and may represent another species.

Material examined for Schmelzmuster.—An M_2, UNSM 47703, from the Seneca Local Fauna, Hooker County, Nebraska.

Description of diagnostic dental characters.—The general features of *M. vetus* may be found in Zakrzewski (1972). The Schmelzmuster of *Metaxyomys vetus* shows a leading edge similar to that in other Lemminae. More than 50% of the total thickness (80 μ) is lamellar enamel. The trailing edges have two thick layers, an inner one of radial enamel and an outer one of lemming enamel of about equal thickness. These layers are widely but not everywhere overlain by a third thin layer of tangential enamel (Fig. 5, A). The trailing edges have a normal thickness of about 80 to 90 μ but thin down near the innermost parts of the synclines to 30 μ.

Discussion.—In *Metaxyomys* the trailing edges of the enamel triangles retain the three layered Schmelzmuster of *Plioctomys.* There is also no significant reduction of enamel thickness except near the deepest parts of the synclines. Some reduction of enamel thickness in this area is the rule among arvicolids with a developed Schmelzmuster. The referred material from the Seneca Local Fauna is smaller than the type material from the Grandview Local Fauna, in the upper part of the Glenns Ferry Formation, Owyhee County, Idaho, and might represent a new species. The differences among the other described species are not very large (Zakrzewski, 1972, fig. 1) and further work needs to be done at the species level in *Metaxyomys.*

Mictomys (*Metaxyomys*) *landesi* Hibbard, 1954

Diagnostic dental characters.—These are summarized by Zakrzewski (1972).

Material examined for Schmelzmuster.—Right M^2 from the Borchers Local Fauna (NAAZ IV), Meade County, Kansas.

Description of the Schmelzmuster.—The Schmelzmuster (Fig. 5, B) shows a leading edge of about 70 μ of which a little more than 50% is lamellar enamel on the inner side. The outer layer is radial enamel. The trailing edges are three-layered with an inner radial enamel overlain by lemming enamel which makes up about one-third of the whole thickness. The outer layer is radial or tangential enamel. The total thickness of the trailing edges ranges from 70–80 μ.

Mictomys (*Metaxyomys*) *anzaensis* Zakrzewski, 1972

Discussion.—No specimens of this species were examined by us and we have nothing to add to Zakrzewski's comments.

Kentuckomys, new subgenus

Type species.—*Mictomys* (*Kentuckomys*) *kansasensis* Hibbard 1952.

Diagnosis.—Lemmings with the tooth axis of the lower molars shifted to the labial side; trailing edges extremely reduced on the lower molars with only radial enamel present except near the apex of the lingual triangles (Fig. 5, D); incisor terminating posteriorly at about the position of the first reentrant of M_3.

Mictomys (*Kentuckomys*) *kansasensis* Hibbard, 1952

Material examined for Schmelzmuster.—One lower M_1 each from the Kentuck (type locality), Wathena, and Sappa Local Faunas and one M^1 each from the Kentuck and Wathena Local Faunas.

Description of the Schmelzmuster.—The lower molars have triangles with leading edges from 70 to 80 μ thick, with about 50% of this thickness an inner layer of typical lamellar enamel. The outer layer is radial enamel. The trailing edges are extremely reduced. Near their lingual border they are around 50 μ thick and contain some lamellar enamel on the inside. The enamel thins rapidly to about 30 μ and then gradually to the inner part of the triangles where the thickness becomes less than 10 μ. The whole length except the previously mentioned lingual margin is exclusively radial enamel (Fig. 5, C) as is the case for the closing enamel of the posterior loop.

The strongly reduced labial triangles are divided by shallow valleys. The first valley shows the normal differentiation between leading and trailing edges, but the second and third have lamellar enamel along the whole length of their enamel band.

The upper molars differ from the lower ones in having much less shifting of the tooth axis. The shift in upper molars is to the lingual side causing deeper labial synclines than lingual ones. The labial ones

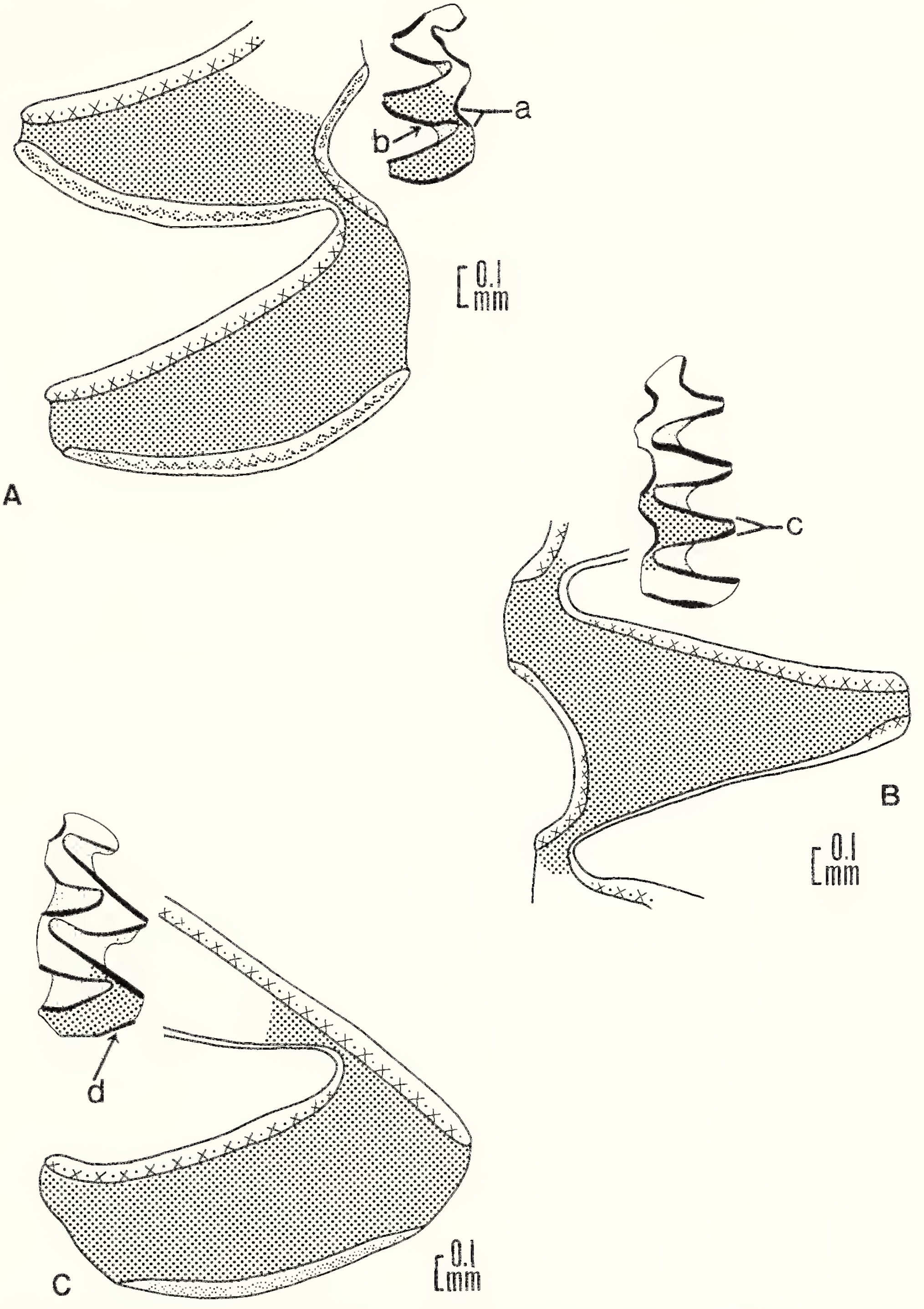


Fig. 6.—Schematic drawings of Schmelzmusters in *Mictomys*. A. *Mictomys* (*Metaxyomys*) *vetus*, right M_2 (a = location of Fig. 2, A; b = location of Fig. 5, A). B–C. *Mictomys* (*Kentuckomys*) *kansasensis*. B. Left M_1 (c = location of Fig. 5, D). C. Right M^1 (a = location of Fig. 5, E).

have a Schmelzmuster similar to that of the lingual ones in the lower molars. The labial triangles occasionally show a less reduced trailing edge with two layers consisting of lemming enamel on top of radial enamel. The closing enamel of the anterior loop shows three layers: an inner radial one, a layer of lemming enamel, and an outer layer of radial enamel (Fig. 5, E).

SUMMARY AND CONCLUSIONS

The Lemminae developed superhypsodonty and a differentiated Schmelzmuster at a very early stage in their evolutionary development. No predecessors with rooted molars are known, although the Lemminae extend at least back to the Middle Villafranchian in Europe. The North American form *Synaptomys* (*Plioctomys*) *rinkeri* is only slightly younger in age, and the near-simultaneous appearance of the Lemminae in North America and Europe without antecedents argues for an origin of the group in northern Asia and a subsequent southern range extension. *Synaptomys* (*Plioctomys*) is a little older than *Lemmus* as presently known and the alternating arrangement of the second labial and first lingual reentrants in M^3 should be primitive. *Lemmus* had already modified this arrangement so that the reentrants are opposing by the late Middle Villafranchian. Although *Lemmus* is in some ways the least modified living lemming, *Synaptomys* (*Plioctomys*) could well be the most primitive known lemming. The shift of the tooth axis in this form reported by Kowalski (1977) is very unclear in his figures, a shift is distinctly present in the North American form *S.* (*P.*) *rinkeri.* Something close to *S.* (*Plioctomys*) *rinkeri* may have given rise to the later bog lemmings of North America including both the later *Synaptomys* and *Mictomys* groups. Except for reduction in the enamel of the trailing edges on the molars, *Synaptomys* (*Synaptomys*) is little modified dentally from *S.* (*Plioctomys*).

The only Pleistocene record of *Lemmus* south of the continental ice sheet in North America was recently reported from the late Pleistocene (22,000–23,000 y.b.p.) of January Cave in Southwestern Alberta (Burns, 1980). This suggests that *Lemmus* expanded its range south at about the same time as *Dicrostonyx* did. The northern bog lemming group appears a little later than *S.* (*Plioctomys*) *rinkeri* and although both southern bog lemming and northern bog lemming groups must co-exist temporally at this time they are not found together in the same local faunas. The earliest northern bog lemming is *Mictomys* (*Metaxyomys*) *vetus* known from the NAAZ III of Idaho and probably Nebraska. Another form *M.* (*Metaxyomys*) *anzaensis* occurs as far south as California indicating a very wide latitudinal range for *Metaxyomys. Mictomys* (*Metaxyomys*) *anzaensis* may be more nearly contemporary with *M.* (*Metaxyomys*) *landesi* from Meade County, Kansas (Hibbard, 1954; see Martin, 1979, for a discussion of the relative ages of these faunas).

Mictomys (*Metaxyomys*) retains the primitive lemming enamel structure but has carried the shift of the tooth axis to the point where the first and second alternating triangles of the lower molars are confluent, a major character uniting all northern bog lemmings (see Fig. 7, character 3). This confluency is the result of shortening of the first labial reentrant angle. In *M.* (*Metaxyomys*) *vetus,* where the character can be checked, the lower incisor has already been shortened to a point beneath the anterior end of M_3. However, we cannot be sure that this position holds for all species within the subgenus. This is an important point because the next oldest known northern bog lemming *M.* (*Kentuckomys*) *kansasensis* retains the primitive positioning of the lower incisor (Hibbard, 1952). This subgenus cannot be considered ancestral to later species of *Mictomys* as it couples its primitive incisor position with the most advanced enamel reduction known in the Lemminae. It must instead be regarded as an endemic midwestern branch which became extinct before the immigration of *M.* (*Mictomys*) line to that region.

We must suppose that a separate branch including the ancestor of *Mictomys* (*Mictomys*) *meltoni* existed elsewhere at this time, perhaps in the poorly sampled faunas of the Northeast. Unfortunately, faunas of this age are not certainly known from that area. *Mictomys* (*Kentuckomys*) occurs with the Holarctic genus *Allophaiomys* in the Wathena and Kentuck Local Faunas in Kansas and in the Sappa and McCook Local Faunas in Nebraska. At the present time no *Synaptomys* (*Synaptomys*) of this age (NAAZ IV) has been recognized. By NAAZ V the northern bog lemming in Kansas and Nebraska is *Mictomys* (*Mictomys*) *meltoni* a form distinguished from *M.* (*Kentuckomys*) *kansasensis* by the more anterior termination of its lower incisor and by having two layers of enamel on the trailing edges of its molar enamel. *M.* (*Mictomys*) *borealis* probably appears in Nebraska in the Bartek Brothers Local Fauna in NAAZ VI and is not uncommon in NAAZ VII faunas in the northeast.

In *M. meltoni* the second labial reentrant fold shows a differentiation between trailing edge and leading edge which is lost with the shallowing of this fold in *M. borealis.* The functional aspects of the shift of the tooth axis is not yet studied, but it is

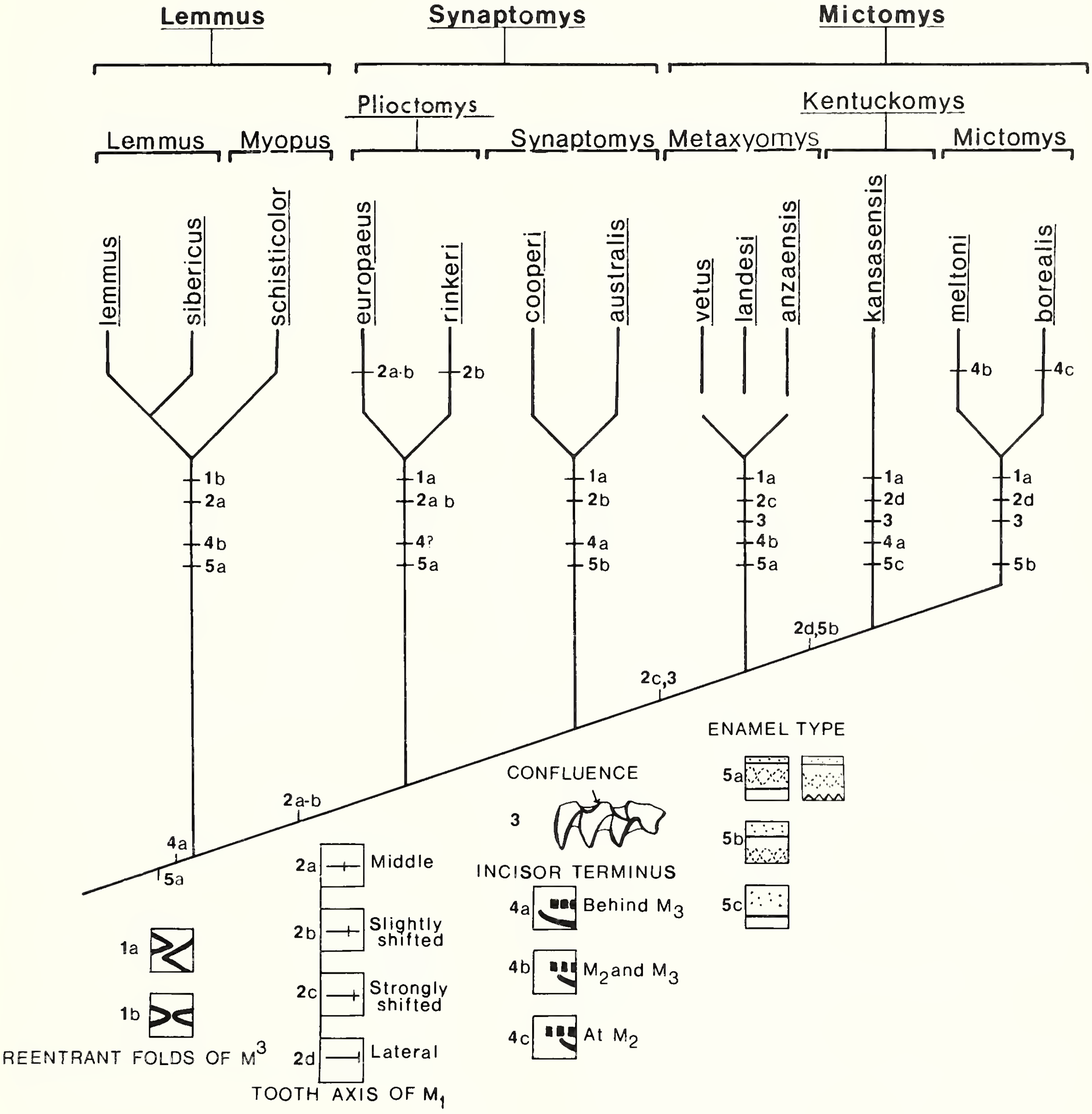


Fig. 7.—Cladogram showing suggested relationships and distribution of characters within the Lemminae. Character 1 contrasts alternating synclines in M^3 (1a) with opposing synclines (1b) (the more derived the character the later the letter [from a–d] associated with it). Character 2 is the progressive shifting of the tooth axis on M^1 (as defined as the place where lingual and labial synclines tend to meet) towards the labial side of the tooth. Character 3 is the development of a broad confluence between the first and second alternating triangles on M_1–M_3 (arrow gives the location of this confluence). Character 4 involves the progressive shortening of the incisor so that its posterior terminus becomes progressively more anterior. Character 5 is the change in Schmelzmuster brought on by the progressive loss of the outer enamel layers eventually reducing a three-layered trailing edge to a one-layered one.

noteworthy that a second group of the Arvicolidae, the North American genus *Phenacomys*, shows in the lower molars a shift of the axis in the same direction. Among other rodents similar trends can be recognized, one very obvious example is the Caviidae.

Biogeographically, *Mictomys* predominates in the western half of the United States (Idaho, Nebraska, Kansas, and California) until NAAZ VI at which point *S.* (*Synaptomys*) begins to show up in those faunas (for instance the Angus Local Fauna in south-central Nebraska). In the east, *Synaptomys* has a long record in Trout Cave in Virginia from NAAZ V and in Florida from NAAZ VII, suggesting a somewhat later arrival farther south.

The Lemminae may be characterized by shortening of the incisors and the development of lemming enamel. The relationships of the genera and subgenera may be worked out by the distribution of character states in: (1) the reentrant folds of M^3; (2) the tooth axis of M_1; (3) the confluence of the first and second triangles of the lower molars; (4) the position of the posterior end of the lower incisors; and (5) the enamel type (Schmelzmuster). In most other arvicolids and in all the Synaptomyini the second and third reentrant folds are alternating. In *Lemmus* these folds oppose each other and this is a derived character for *Lemmus* (Fig. 7, character 1b). The Synaptomyini are united by a slight shift of the tooth axis labially (Fig. 7, character 2b). The subgenus *Plioctomys* does not have a known autapomorphy and therefore fulfills the requirements for an ancestral position to other bog lemmings. The geographic distribution and stratigraphic occurrence of *Plioctomys* is also consistent with such an interpretation. The subgenus *Synaptomys* has a relatively derived Schmelzmuster (Fig. 7, character 5b) but is otherwise fairly primitive. *Synaptomys* must have been separate from the other bog lemmings at least as far back as the Senecan (NAAZ III). The northern bog lemmings (*Mictomys*) are all united by the confluence of the first and second alternating triangles on the lower molars (Fig. 7, character 3). This is a derived character state differing from most other arvicolids. *Mictomys* (*Metaxyomys*) has a primitive Schmelzmuster for a lemming but (in those forms where it can be observed) it may have a slightly advanced positioning of the lower incisor. On the whole it lacks autapomorphies and may be the ancestor of the later *Mictomys*. *Mictomys* (*Kentuckomys*) and *Mictomys* (*Mictomys*) share the most derived state of labial shift of the tooth axis in the lower molars (Fig. 7, character 2d) but *M.* (*Kentuckomys*) couples a very primitive posterior position of the lower incisor terminus (Fig. 7, character 4a) with the most derived Schmelzmuster (Fig. 7, character 5c). It was clearly a side branch.

The historical biogeography of the Lemminae in North America is of some interest. The earliest northern bog lemmings, *Mictomys* (*Metaxyomys*), have an enormous range, occurring during NAAZ III from as far south and west as southern California to as far north as Idaho, Kansas and Nebraska. During this same time *Synaptomys* (*Plioctomys*) occurred in Kansas (Dixon and White Rock Local Faunas). There are no records of southern bog lemmings during NAAZ IV but *Mictomys* (*Kentuckomys*) is known from South Dakota, Nebraska, and Kansas. During NAAZ V *Lemmus* appears in Alaska and true northern bog lemmings, *Mictomys* (*Mictomys*), occur as far south as southern Kansas. During NAAZ VI both *Mictomys* and *Synaptomys* occur in Nebraska and *Synaptomys* as far south as southern Kansas. In the Wisconsinan *Mictomys* occurs in eastern faunas along the Appalachians and *Synaptomys* as far south as Florida (*Synaptomys australis* Simpson). With the end of the Pleistocene the range of all bog lemmings has become more northerly restricted. Although the ranges of northern and southern bog lemmings overlap each other both temporally and geographically they have not been found together in the same faunas except in the eastern part of the United States, where *Mictomys* (*Mictomys*) is found with *Synaptomys* (*Synaptomys*) during NAAZ VII. *Mictomys* (*Mictomys*) also occurs in Cumberland Cave in Maryland during NAAZ V, and although it is closely similar to *M. meltoni* which occurred at the same time in the central Great Plains, it is more similar to *M. borealis* (Van der Meulen, 1978). *Synaptomys* occurs in Trout Cave in West Virginia during NAAZ V and it seems likely that the modern species of bog lemmings were derived from Appalachian stock during the Wisconsinan.

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LITERATURE CITED

Agadjanian, A. K., and W. v. Koenigswald. 1977. Merkmalsverschiebung an den oberen Molaren von *Dicrostonyx* (Rodentia, Mammalia) im Jungquatär. N. Jb. Geol. Palaont. Abh., 153:33–49.

Burns, J. A. 1980. The brown lemming, *Lemmus sibiricus* (Rodentia, Arvicolidae), in the late Pleistocene of Alberta and its postglacial dispersal. Canadian J. Zool., 58:1507–1511.

Chaline, J. 1972. Les rongeurs due Pléistocène moyen et supérieur de France. Cah. Paléont., C.N.R.S., Paris, 410 pp.

Eshelman, R. E. 1975. Geology and paleontology of the early Pleistocene (late Blancan) White Rock fauna from north-central Kansas. Univ. Michigan Mus. Paleont., Papers in Paleont., no. 13:1–60.

Greaves, W. S. 1973. The inference of jaw motion from tooth wear facets. J. Paleont., 47:1000–1001.

Guthrie, R. D., and J. V. Matthews, Jr. 1971. The Cape Deceit Fauna: Early Pleistocene mammalian assemblage from the Alaska Arctic. Quaternary Res., 1(4):474–510.

Hibbard, C. W. 1952. Vertebrate fossils from late Cenozoic deposits of central Kansas. Univ. Kansas Paleont. Contrib., art. 2:1–14.

———. 1954. A new *Synaptomys*, an addition to the Borchers interglacial (Yarmouth?) fauna. J. Mamm., 35:249–252.

———. 1956. Vertebrate fossils from the Meade Formation of southwestern Kansas. Papers Michigan Acad. Sci. Arts and Letters, 41:145–200.

Howell, A. B. 1927. Revision of the American lemming mice. North American Fauna, no. 50:1–38.

Koenigswald, W. v. 1973. Veränderungen in der Kleinsaugerfauna von Mitteleuropa zwischen Cromer und Eem (Pleistozän). Eiszeitalter u. Gegenwart, 22/23:159–167.

———. 1977. *Mimomys* cf. *reidi* aus der villafranchischen Spaltenfüllung Schambach bei Treuchtlingen. Mitt. Bayer. Staatsslg. Paläont. Hist. Geol., 17:197–212.

———. 1980. Schmelzstruktur und Morphologie in den Molaren der Arvicolidae (Rodentia). Abh. Senckenb. Naturforsch. Ges., 539:1–129.

Kowalski, K. 1977. Fossil lemmings (Mammalia, Rodentia) from the Pliocene and early Pleistocene of Poland. Acta Zool. Cracov., 22:297–317.

Martin, L. D. 1979. The biostratigraphy of arvicoline rodents in North America. Trans. Nebraska Acad. Sci., 7:91–100.

Miller, G. S. 1912. Catalogue of the mammals of western Europe (Europe exclusive of Russia) in the collection of the British Museum. British Museum (Natural History), 1,019 pp.

Paulson, G. R. 1961. The mammals of the Cudahy fauna. Papers Michigan Acad. Sci., 46:127–153.

Rausch, R. L. 1978. Systematic position of *Dicrostonyx* Gloger, 1841. Abstracts of meeting, Amer. Quaternary Assoc., p. 81.

Schultz, C. B., L. D. Martin, L. G. Tanner, and R. G. Corner. 1978. Provincial land mammal ages for the North American Quaternary. Trans. Nebraska Acad. Sci., 5:59–64.

Semken, H. A., Jr. 1966. Stratigraphy and paleontology of the McPherson *Equus* beds (Sandahl Local Fauna), McPherson County, Kansas. Contr. Mus. Paleont., Univ. Michigan, 20: 121–178.

Sukhov, V. P. 1976. [Fossil lemmings in the Pleistocene Strata of Rashkiria.] *In* [Rodents: evolution and history of their Recent fauna.] Proc. Zool. Inst. Acad. Sciences USSR, 66: 117.

Terzea, E. 1972. Sur la presence du genre *Lemmus* (Rodentia, Mammalia) dans le Pleistocene de la Roumanie. Folia. Quat., 40:57–65.

Van der Meulen, A. J. 1978. *Microtus* and *Pitymys* (Arvicolidae) from Cumberland Cave, Maryland, with a comparison of some New and Old World species. Ann. Carnegie Mus., 47:101–145.

Wilson, R. W. 1932. *Cosomys*, a new genus of vole from the Pliocene of California. J. Mamm., 13:150–154.

———. 1933. A rodent fauna from later Cenozoic beds of southwestern Idaho. Carnegie Inst. Washington, Publ. 440:117–135.

———. 1937. New Middle Pliocene rodent and lagomorph faunas from Oregon and California. Carnegie Inst. Washington, Publ. 487:1–19.

Zakrzewski, R. J. 1972. Fossil microtines from late Cenozoic deposits in the Anza-Borrego Desert, California, with the description of a new subgenus of *Synaptomys*. Contrib. Sci., Mus. Nat. Hist. Los Angeles County, no. 221:1–12.

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EOCENE CTENODACTYLOID RODENTS (MAMMALIA) OF EASTERN AND CENTRAL ASIA

MARY R. DAWSON, CHUAN-KUEI LI, AND TAO QI

ABSTRACT

A review of the Eocene rodent record of China, including Inner Mongolia, illustrates the dominance of the Ctenodactyloidea, a superfamily here used to include the new Eocene families Cocomyidae and Yuomyidae, in addition to the Oligocene to Recent Ctenodactylidae. The Eocene family Chapattimyidae of India and Pakistan is probably also ctenodactyloid. The line leading to the Recent family Ctenodactylidae can now be traced to the early Eocene. A new generic name, *Cocomys,* is provided for the early Eocene species, *Microparamys lingchaensis* Li, Chiu, Yan, and Hsieh, and new species of *Advenimus* and *Tamquammys* are described. The ctenodactyloid radiation in Asia is discussed in morphological and phylogenetic relation to the Eocene rodent record elsewhere.

INTRODUCTION

One of the most puzzling groups of rodents has been the superfamily Ctenodactyloidea, having a single Recent family, the Ctenodactylidae. Simpson (1945), with his usual insight, put the ctenodactyloids in proper perspective, stating that, "the group vies with or exceeds the bathyergids in uncertainty." When Simpson wrote, he recognized no extinct genera of ctenodactylids, although three extinct genera now considered ctenodactylids, *Tataromys, Karakoromys,* and *Sayimys,* were included in his classification. The first two had been described as ?Eomyidae (Matthew and Granger, 1923), considered near the Theridomyidae (Teilhard, 1926), and were treated by Simpson (1945:82–83) as cf. ?Theridomyidae *incertae sedis.* The last was first recognized as a ctenodactylid (Hinton, 1933:622) but later given no familial or subordinal assignment. It was considered probably somewhat like various "Hystricomorpha" (Wood, 1937), and treated by Simpson (1945:99) as ?Thryonomyidae *incertae sedis.* Bohlin's thorough analysis (1946) of *Tataromys, Karakoromys,* and *Sayimys* from western Kansu led to the recognition that these genera are ctenodactylids and have nothing to do with the Theridomyidae and Eomyidae. Now, 16 additional genera, ranging in age from Eocene to Pleistocene, have been referred to the Ctenodactylidae (Wood, 1977), although, true to tradition, several of them were originally assigned to other families (Bohlin, 1946; de Bruijn and Rümke, 1974; Dawson, 1964; Gregorio, 1887; Jaeger, 1971; Lavocat, 1961; Li, 1963; Robinson and Black, 1973; Shevyreva, 1971*a,* 1971*b,* 1972).

In spite of this relatively impressive fossil record, the ctenodactyloids have remained a group of uncertain position relative to other rodents. The four Recent genera of ctenodactylids, *Ctenodactylus, Pectinator, Massoutiera,* and *Felovia,* are limited geographically to Africa north of the equator. There is no convincing evidence for close affinities of these ctenodactylids with other Recent rodents. Their morphological combination of an hystricomorphous skull and sciurognathous, though highly modified, jaw is shared with the African Anomaluridae and Pedetidae and the Holarctic and North African Dipodoidea. Their multiserial incisor enamel is found also in the Pedetidae, but the combination of reduced premolars, relatively large $M\frac{3}{3}$, obliquely lophate molars, and jaw with reduced coronoid process and low condyle is found only in the ctenodactylids. The Recent ctenodactylids that have been studied for parts of their soft anatomy show some probably primitive features (for example, various characters of the fetal membranes in *Ctenodactylus*: Luckett, 1971) but also some specializations (for example, cephalic arterial system in *Pectinator*: Guthrie, 1963; Bugge, 1974). The total picture presented by the Recent cetnodactylids is one of distinction from other rodents. The now known fossil record emphasizes that at least some of the distinctions of their relatives extend into the Eocene.

This paper began simply as a description of a new species from Inner Mongolia of the Eocene ctenodactyloid *Tamquammys.* From that straightforward beginning it grew into a review of the eastern and central Asian Eocene ctenodactyloids. The review led to the conclusion that morphological variation and lines of divergence seen in the Eocene record were too great to allow inclusion of the Eocene forms in the single family Ctenodactylidae, and two additional ctenodactyloid families are proposed below. This study is based primarily on specimens from China, including Inner Mongolia, in the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing (IVPP). Remarks on fossils from other parts of Asia are based on casts and on information from the literature.

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We especially thank Robert W. Wilson, whose guidance and example led us in tracing one more convolution of rodent evolution. Zheng Jia-jian kindly permitted us to examine excellent specimens collected in Hunan that will be the objects of later detailed study by him and Li. We thank Drs. Wilson, Craig Black, and William Korth for their critical readings of this paper and Chow Minchen for doing so much to further studies of Asian fossil mammals. We appreciate the loan of comparative specimens from the American Museum of Natural History (AMNH). The illustrations were skillfully prepared by William Korth.

THE RECORD OF EOCENE CTENODACTYLOIDS IN EASTERN AND CENTRAL ASIA

A certain amount of readjustment will undoubtedly be made in regard to estimation of the ages of some Eocene horizons in Asia relative to those elsewhere. Current work in Inner Mongolia (Qi, 1979) is clarifying stratigraphic relationships within that region, but details of correlation between Inner Mongolia, Mongolia, Kazakhstan, and more southerly parts of China remain to be established. The problems are especially acute for the middle and late Eocene. In this paper, those faunas here considered referable to the time intervals mentioned are listed to avoid possible misunderstanding.

The family Ctenodactylidae was used by Wood (1977) to include the Asian Eocene genera *Saykanomys, Advenimus, Tsinlingomys,* and *Yuomys,* distributed in China, Mongolia, and Kazakhstan. Though none is very completely known, these genera resemble the later ctenodactylids in some dental features including, most consistently, increase in size posteriorly of the molars and emphasis on a large hypoconulid-posterolophid. Those known by partial skulls, *Saykanomys* and *Yuomys,* are hystricomorphous; all are sciurognathous. Some specimens of *cf. Advenimus* have a lower jaw with the area for masseter muscle insertion suggestive of that in the later ctenodactylids. The rodents here reviewed as ctenodactyloids include these four genera as well as several others that have the dental features mentioned plus upper molars with a hypocone that is separate from the metacone-metaloph. They also have well developed conules, and lower molars with metalophulid I forming the anterior wall of the molar and a short posterior arm of the protoeonid. Eocene rodents having these basic dental features are known also from farther south, in India (Sahni and Khare, 1973; Sahni and Srivastava, 1976) and Pakistan (Hussain and others, 1978). They are probably also ctenodactyloids and will be mentioned again below in the discussion of the affinities of the central and eastern Asian ctenodactyloids.

EARLY EOCENE

(fauna of upper level, Hengtung County, Hunan)

The only ctenodactyloid reported from definitely early Eocene deposits in Asia is from Hunan in southern China (Li and others, 1979). The associated fauna suggests an age equivalent to Cuisian or Sparnacian. The rodent, known originally from two lower jaws, was referred to as a new species of the ischyromyid genus *Microparamys, M. lingchaensis.* Additional, excellent material of this species and a closely related one, collected by Zheng and colleagues, is under study by Zheng and Li and will be described elsewhere. In the meantime, a new generic name is here provided for *M. lingchaensis,* which is not *Microparamys* but is rather the oldest known ctenodactyloid.

Cocomys, new genus

Type species.—*Microparamys lingchaensis* Li, Chiu, Yan, and Hsieh (1979:76).

Etymology.—In honor of the late C. C. Young, distinguished scholar and eminent paleontologist, coining the name from the initials C. C.

Diagnosis.—Rodent with skull protrogomorphous, infraorbital foramen not enlarged; jaw sciurognathous, coronoid process high, condyle well above level of tooth row, masseteric fossa deep, bordered by dorsal and ventral ridges, of which dorsal is heavier, extends to below M_{2-3}. Dental formula $\frac{1}{1}, \frac{0}{0}, \frac{2}{1}, \frac{3}{3}$. Cheek teeth increase in size from front to back. DP^4 molariform; P^4 not molariform, having single buccal cusp. Upper molars with well developed conules, hypocone present, metaloph directed toward protocone. P_4 having trigonid slightly wider than talonid, protoconid and metaconid well developed, metaconid larger; posterior border of talonid formed by anteroposteriorly narrow, transversely elongate crest connected to elongated entoconid. Lower molars have: anterior wall formed by connection of protoconid and metaconid as metalophulid I; short posterior arm of protoconid; rounded mesoconid; posterior cingulum set off by groove from hypoconid; prominent, elongated hypoconulid.

Referred species.—Type species only.

Cocomys lingchaensis (Li, Chiu, Yan, and Hsieh, 1979)

Type specimen.—IVPP V5347, left lower jaw with P_4–M_3.

Referred specimen.—IVPP V5348, left lower jaw with P_4–M_3.

Horizon and locality.—Early Eocene; locality 76003, Hengtung County, Hunan, China.

Diagnosis.—Only described species of genus; see generic description.

Discussion.—A more complete description of the skull and upper dentition of *Cocomys* will be made later by Zheng and Li. At present the diagnostic characters given above and the previous description (Li and others, 1979) clearly indicate the characters that differentiate *Cocomys* from *Microparamys* and suggest its affinities with the ctenodactyloids. *Cocomys* is distinguished from *Microparamys* on the basis of the following characters of lower cheek teeth of the former: proportions within tooth row with increase in size from P_4 to M_3; P_4 with trigonid well developed relative to talonid; molars having a strong metalophulid I but lacking an anterior cingulum; cuspate entoconid; posterior cingulum set off from hypoconid; prominent hypoconulid (Fig. 3E). Dental features of *Cocomys* that support alliance with ctenodactyloids are the increase in size posteriorly of the cheek teeth, P^4 with one buccal cusp, orientation of lophs toward protocone on upper molars, relatively small talonid of P_4, and prominence of the hypoconulid in the lower molars. That *Cocomys* is distinctly more primitive than other ctenodactyloids is shown most clearly by its protrogomorphous zygomasseteric structure and also by relatively slight development of lophs.

LATE EARLY OR EARLY MIDDLE EOCENE

(Yu-huang-ding, Hubei)

A new, primitive species of the ctenodactyloid *Advenimus* occurs in a locality in Hupei that was described by Xu and others (1979). This is the only rodent presently known from deposits that also yield the peculiar gliriform anagalid *Rhombomylus.*

Advenimus hupeiensis, new species

Type specimen.—IVPP no. 5248, right jaw with broken P_4, M_{1-3}.

Referred specimens.—IVPP nos. 5249, right jaw with worn P_4–M_3; 5250, left jaw with crowns of cheek teeth broken off.

Age and locality.—Late early or early middle Eocene; Yu-huang-ding Fm., Da-jian village, Xi-jiadian commune, Hubei; field no. 76006(80).

Diagnosis.—Species of *Advenimus* near *A. burkei* in size. P_4 with talonid wider than trigonid, hypoconid better developed than in other species of genus, relatively shorter anteroposteriorly than in *A. bohlini.* M_{1-2} have distinct anterior and posterior arms of protoconid, rounded mesoconid on ectolophid; entoconid not strongly crested. Masseteric fossa farther posterior than in other species of genus.

Description.—The known specimens, all incomplete jaws, show a distinct masseteric fossa that extends forward to a line between M_{2-3} and is delimited by an anterodorsal and a stronger ventral ridge. The coronoid process rises well above the tooth row.

The little worn teeth of IVPP no. 5248 (Fig. 1A) have the basic ctenodactyloid features of increase in size posteriorly and well developed hypoconulids. They are markedly cuspate with little development of cresting and lophing. On P_4 the well developed trigonid root extends forward beyond the crown. An unworn P_4 trigonid is unknown, but the posteriorly convex unworn talonid has cuspate hypoconid and entoconid, and enlarged rounded hypoconulid. Following wear (Fig. 1B) P_4 has a wide posterodorsally facing worn surface on the trigonid, which is slightly narrower than the talonid. On M_{1-2} the protoconid has short anterior and posterior arms, which bracket the crest of the metaconid; the ectolophid has a rounded mesoconid. On M_1 the entoconid crest is short, whereas on M_2 there is a more distinct loph extending buccally and curving posteriorly toward

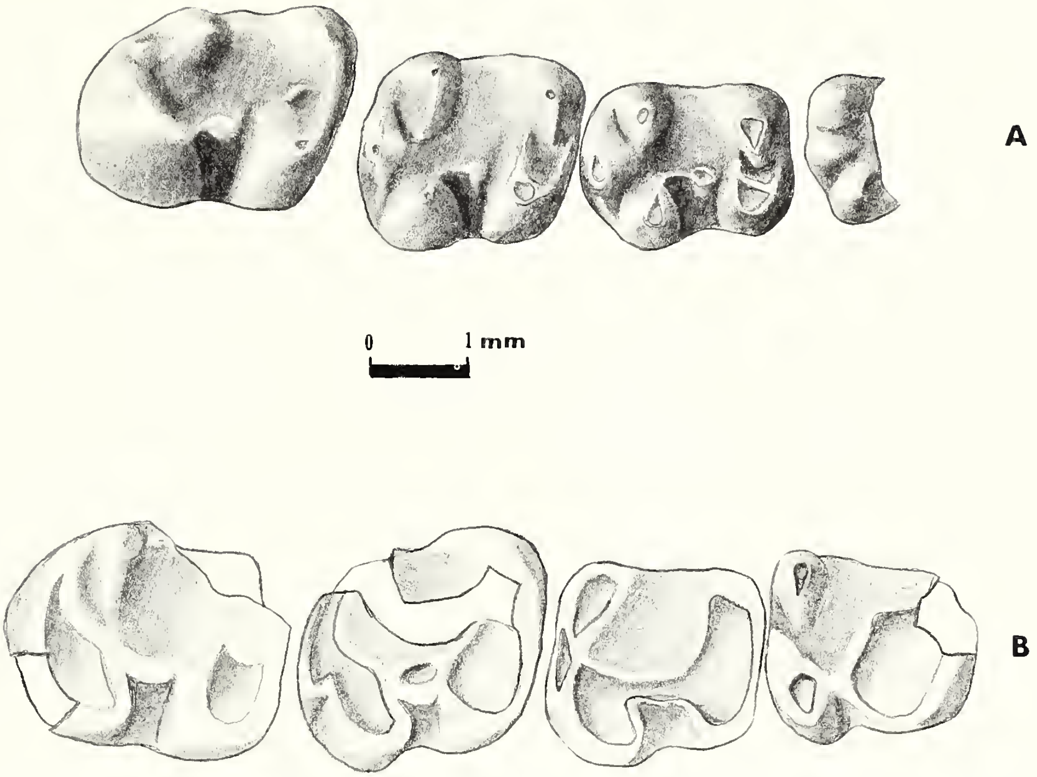

Fig. 1.—*Advenimus hupeiensis.* A. Occlusal view incomplete P_4, M_1–M_3, IVPP 5248, type specimen. B. Occlusal view P_4–M_3, IVPP 5249. ×13.

the hypoconulid. The anterior wall of M_3 is formed by the union of the anterior protoconid arm and the crest of the metaconid (metalophulid I). On this tooth the posterior protoconid arm is short, the ectolophid has only a small swelling indicating a mesoconid, the entoconid has a weak buccal crest, and the posterior wall is formed by a ridge from the hypoconid that joins an elevated cuspule, probably the hypoconulid.

Resemblance to other species of *Advenimus* is shown by the cuspate nature of the teeth and the presence of a hypoconid on P_4. *A. hupeiensis* is more primitive than other species in having less evidence of loph development and the more posterior position of the masseteric fossa. Its measurements are given in Table 1.

Middle Eocene

(Arshanto, Inner Mongolia; Aksyir fauna, Obalia deposits, Kazakhstan)

Tamquammys Shevyreva (1971*a*) is the only ctenodactyloid described from probable middle Eocene deposits of eastern and central Asia. The type species, *T. tantillus,* is from Kazakhstan. Although Wood (1977:126) considered *Tamquammys* to be indeterminate, Shevyreva's genus and species are here considered valid. Discovery of another

Table 1.—*Measurements in mm of* Advenimus hupeiensis.

	Type	
	5248	5249
P_4–M_3 length	—	10.0
P_4 anteroposterior	—	2.15
trigonid width	—	1.75
talonid width	1.55	1.9
M_1 anteroposterior	2.1	2.45
trigonid width	1.6	1.8
talonid width	1.8	2.0
M_2 anteroposterior	2.3	2.6
trigonid width	1.9	2.2
talonid width	2.0	2.3
M_3 anteroposterior	2.6	2.8
trigonid width	2.1	—
talonid width	2.0	2.2

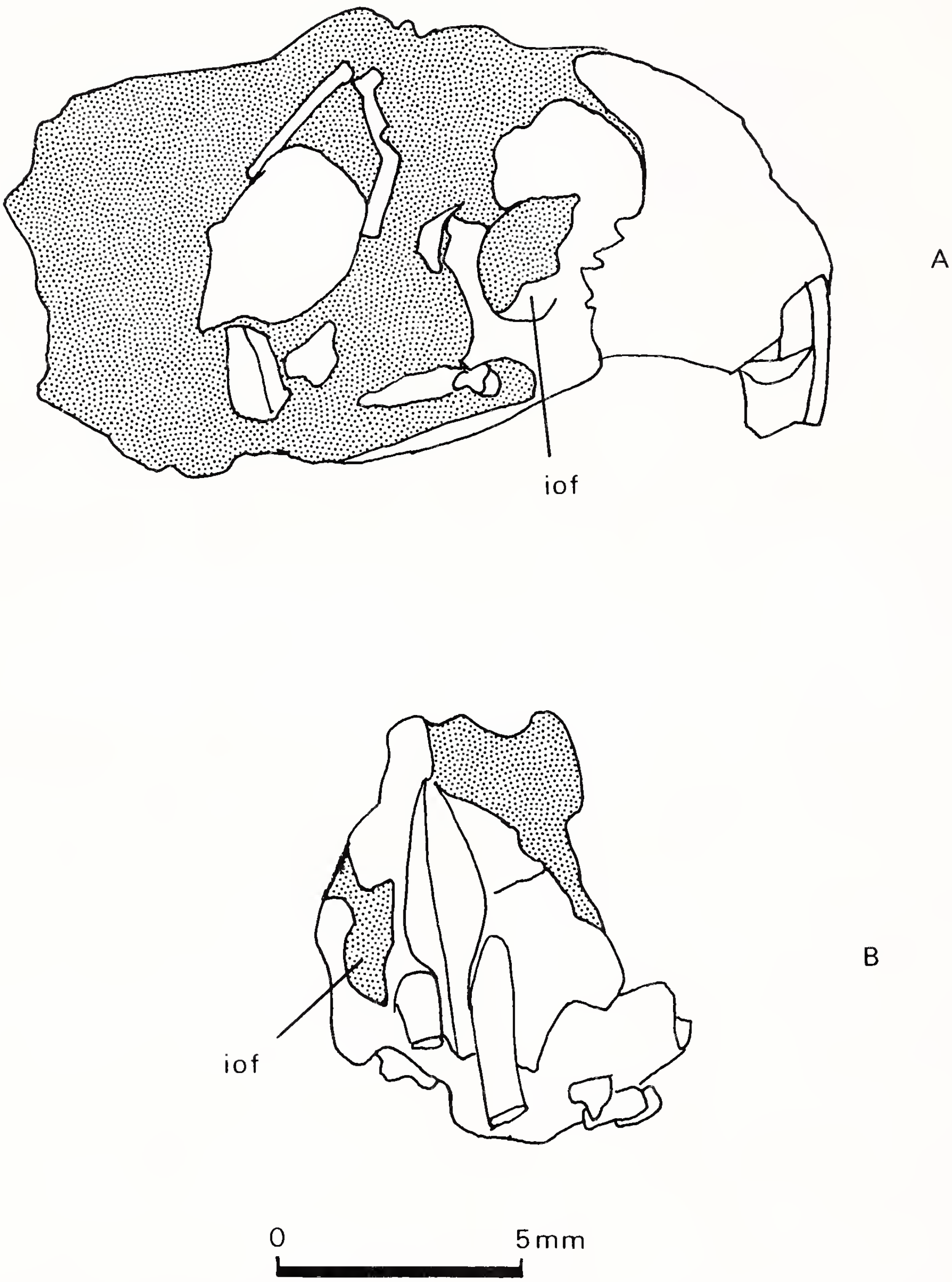

Fig. 2.—*Tamquammys wilsoni*, anterior portion of skull, IVPP V5678, type. A. Lateral view showing infraorbital foramen (iof). B. Anterior view. Approximately ×6.5.

species of the genus in Inner Mongolia extends its geographic range and adds to its known morphology.

Tamquammys Shevyreva (1971)

Type species.—*T. tantillus.* Aksyir, Obaila deposits, Zaysan Basin, Kazakhstan.

Revised diagnosis.—Ctenodactyloid rodent with skull hystricomorphous, lower jaw sciurognathous. Cheek teeth increase in size from front to back, have well developed conules in upper teeth, well developed lophs in lowers. P^4 with single buccal cusp. P_4 with relatively short and narrow talonid.

Distribution.—Middle Eocene. Kazakhstan and Inner Mongolia.

Tamquammys wilsoni, new species

Type specimen.—IVPP no. V5678, anterior portion of skull with broken incisors, right P^4, left dP^3–M^2.

Etymology.—Named in honor of Robert W. Wilson.

Referred specimens.—IVPP nos. V5679, right jaw with I, P_4–M_3; V5680, right jaw with M_{1-3}; V5683, left lower molar. All specimens came from one bony nodule.

Horizon and locality.—Arshanto, middle Eocene. Camp Margetts area, Inner Mongolia.

Diagnosis.—Smaller than *T. tantillus*; P_4 has talonid less well developed posterobuccally, hypoconid-hypoconulid ridge more oblique, less transverse in orientation.

Description.—The incomplete skull (Fig. 2) is distorted both by lateral crushing and by some anteroposterior compression that has pushed the left auditory bulla anteriorly. The premaxilla is high dorsoventrally. The infraorbital foramen is large. The maxilla has a low ridge dorsomedial to the foramen and a depression, both of which seem to indicate the limits of origin for the part of the masseter medialis that passes through the foramen. The anterior root of the zygoma extends laterally in a line just anterior to P^3.

Lower jaw.—Neither jaw is complete. The masseteric fossa extends forward to below the talonid of M_2, the ridge forming its lower margin extending slightly farther forward to a rounded termination.

Dentition.—Upper and lower incisors are narrow transversely, with the former more curved on the lateral side, the latter more flattened. The individual represented by V5678 is immature, still having left dP^{3-4} (Fig. 3A); on the right side the completely unworn P^4 is preserved in its socket (Fig. 3B). The deciduous teeth are the first known for *Tamquammys.* DP^3 has a single cusp and a posterior cingulum, which is widest lingually, forming a buccally slanting shelf. DP^4, set somewhat obliquely in the tooth row, is basically a molariform tooth, with subequal paracone and metacone, well developed protocone and smaller hypocone. The conules are distinct; the protoconule forms part of a ridge extending from the protocone to the anterolingual side of the paracone, and the metaconule is part of the ridge from the metacone to the posterolingual slope of the protocone. The hypocone appears as a lingual development on the posterior cingulum.

Table 2.—*Measurements in mm of* Tamquammys wilsoni.

		V5678	V5679
dp^4	anteroposterior	1.2	—
	transverse	1.7	—
P^4	anteroposterior	1.2	—
	transverse	1.8	—
M^1	anteroposterior	1.4	—
M^2	anteroposterior	1.5	
P_4–M_3	length	—	6.7
P_4	anteroposterior	—	1.5
	trigonid width	—	1.1
	talonid width	—	0.9
M_1	anteroposterior	—	1.5
	trigonid width	—	1.3
	talonid width	—	1.5
M_2	anteroposterior	—	1.7
	trigonid width	—	1.5
	talonid width	—	1.6
M_3	anteroposterior	—	1.9
	trigonid width	—	1.6
	talonid width	—	1.5

Unworn P^4 has the tip of the paracone broken but is otherwise complete. This tooth, relatively short anteroposteriorly and wide transversely, has well developed anterior and posterior cingula. There is one buccal cusp and a protocone, between which there are anterior and posterior ridges each with a conule, the larger one posterior. The hypocone is a small cusp on the lingual end of the posterior cingulum.

The two upper molars preserved are both broken buccally, with the metacone gone from M^1 and both buccal cusps from M^2. These teeth are characterized by a well developed anterior cingulum, elongated protoconule and larger, rounded metaconule on lophs extending from the buccal cusps to the protoeone. The distinct hypocone, which tends to square up the lingual wall, is smaller than the protocone and situated at the lingual end of the posterior cingulum. A ridge from the protocone joins one from the hypocone, forming the edge of the lingual valley. The molars exhibit a slight lingual hypsodonty.

The lower cheek teeth (Fig. 3C, D) have a number of distinctly ctenodactyloid characteristics. The most obvious of these is the structure of P_4, which has a better developed trigonid than talonid. Protoconid and metaconid are prominent cusps, which rise steeply above the talonid. The relatively low, narrower talonid has a cuspate entoconid and an

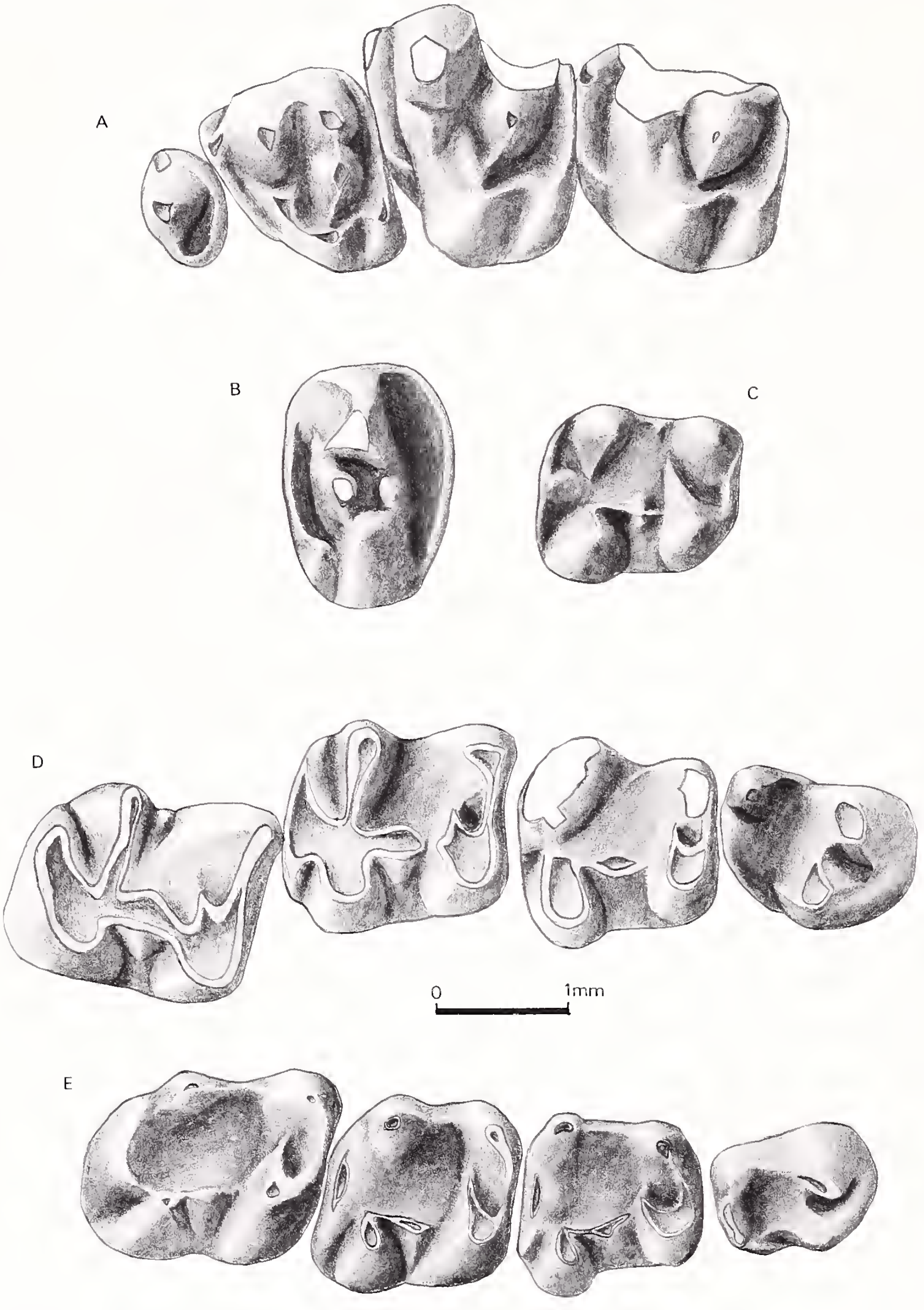

Fig. 3.—A–D. *Tamquammys wilsoni,* occlusal views of teeth. A. Left dP^3–M^2, IVPP V5678, type. B. Right P^4, IVPP V5678. C. Right lower molar, IVPP V5683. D. Right P_4–M_3, IVPP V5679. E. *Cocomys lingchaensis,* occlusal view, right P_4–M_3 (reversed), IVPP V5347, type. ×18.

obliquely oriented posterobuccal side, which seems to be formed by a posterolophid. The molar trigonids have a ridge-like anterior wall formed by a ridged metaconid, which joins the anterior protoconid arm forming a metalophulid I. The posterior protoconid arm is short. The ectolophid includes a rounded mesoconid. On M_1 the hypolophid extends somewhat posterobuccally from the entoconid to the hypoconid, whereas on M_{2-3} it extends more transversely to the hypoconid. The posterior cingulum is prominent, extending both buccally and lingually from a large, cuspate hypoconulid. On M_3 the posterior cingulum-hypoconulid projects posteriorly, rounding off the back of the tooth row.

The measurements of *T. wilsoni* are given in Table 2.

EARLY LATE EOCENE

(includes Lushih and Haitaoyuantze, Honan; Irdin Manha and Ulan Shireh, Inner Mongolia; Khaytshin-Ula II, Mongolia; Aksyir and Ulken-Ulasty, Kazakhstan)

The greatest diversity in Eocene ctenodactyloids occurs in this interval, although the localities may span a considerable time.

Advenimus Dawson (1964) is represented by two named species, *A. burkei* and *A. bohlini,* and several specimens without species reference. This was the first genus of Eocene ctenodactyloid to be described; it was originally referred with question to the Sciuravidae, but ctenodactyloid affinities were suggested. As with the earlier species, *Advenimus hupeiensis,* these species are known only from lower jaws. Their ctenodactyloid nature is shown by the proportions of the molars, large hypoconulid, and P_4 with the talonid not strongly developed (slightly narrower than the trigonid in *A. burkei,* slightly wider in *A. bohlini*; X-ray photographs taken of the jaws of both species show that the premolars are permanent ones). In *Advenimus* cusps are emphasized over crests, a development different from that shown by *Tamquammys.* The premolar talonid is better developed than in *Cocomys* and *Tamquammys,* having more similarity to those in *Petrokozlovia* and *Yuomys.* Presence of the hypoconid on P_4 also suggests that P^4 in *Advenimus* had a metacone.

Saykanomys chalchae Shevyreva (1972), from Mongolia and Kazakhstan, though originally described as a sciuravid, has been shown to have ctenodactyloid characteristics (Dawson, 1977; Wood, 1977). The zygomasseteric structure is hystricomorphous-sciurognathous. In molar morphology *Saykanomys* has well developed conules, strong metalophulid I, large hypoconulid, and other features of resemblance to *Tamquammys.* P^4 is molariform, with well developed anterior cingulum, paracone and metacone both present, and distinct hypocone; P_4 is elongated anteroposteriorly and has a wider talonid than trigonid. Comparison of the figure of the type lower jaw of *Saykanomys chalchae* (Shevyreva, 1976:28 and plate 1, fig. 4) with the type of *Advenimus bohlini,* AMNH 26294, shows a striking similarity in size and morphology of jaw and teeth. Although it is somewhat hazardous to propose identity without examining the type of *Saykanomys chalchae* itself, it appears highly likely that it is synonymous with *A. bohlini.*

Petrokozlovia notos Shevyreva (1972), from Mongolia and Kazakhstan, is another hystricomorphous-sciurognathous rodent that was originally described as a sciuravid (Shevyreva, 1972, 1976). Its cheek teeth assume a somewhat cylindrodontid-like appearance when worn, but less worn teeth show a prominence of conules on the upper cheek teeth with the metaconule inclined toward the protocone, the molars increase in size toward the posterior, and the hypoconulid appears to be a prominent structure. P^4 is molariform, with separate, well developed paracone and metacone, and P_4 is a robust tooth, wider in talonid than trigonid and larger than M_1. Thus, *Petrokozlovia* combines several generally ctenodactyloid characters with premolars having basic features of those of *Advenimus* and *Saykanomys.*

Tsinlingomys Li (1963) is a highly distinctive ctenodactyloid, known by lower jaws from the Lushih Formation in Honan. It has an unusual molar pattern with the hypolophid curving back strongly to the hypoconulid. The molars also have a complete metalophulid II. In addition to these distinctions, *Tsinlingomys* has the ctenodactyloid feature of a narrow talonid of P_4 without a hypoconid and molars with well developed metalophulid I and an enlarged hypoconulid.

A single lower molar from Haitaoyuantze, Honan, was referred to as "*Sciuravus* sp." (Li, 1963:154). The complete, strong metalophulid I, short metalophulid II, and large hypoconulid of this tooth are ctenodactyloid features. It does not, however, appear to belong to a taxon known by more complete material.

LATE EOCENE

(Jentsen and Tung-chang, Honan; Ula Usu, Inner Mongolia)

Only one ctenodactyloid, *Yuomys* Li (1975), is known from the latest Eocene of China. This large, hystricomorphous-sciurognathous rodent has the ctenodactyloid features of molars increasing in size toward the posterior, upper molars with large conules, metaloph oriented toward protocone, lower molars with strong metalophulid I, and pronounced hypoconulid. It has large $P\frac{4}{4}$ and the emphasis in dental development is on strong crests, especially in the lower molars. Among the Eocene ctenodactyloids, it is closest to *Petrokozlovia* (Li, 1975:70).

RELATIONSHIPS OF THE EOCENE CTENODACTYLOIDS

Paleontological work during the past 20 years, both field collecting and interpretive studies, has shown that the rodents now recognized as ctenodactyloids played an important role in Asian Eocene faunas. The oldest rodent known from Asia is the early Eocene ctenodactyloid *Cocomys.* In the middle Eocene, morphological developments shown first by *Cocomys* had been further refined in *Tamquammys,* and another line, or lines, of ctenodactyloids had appeared in southern Asia. By the early late Eocene considerable morphological diversity existed among ctenodactyloids.

That, in broadest outline, is the picture presented by the fossil record. Details of interpretation of this record need further discussion, especially those centered around the following questions. (1) What is the position of *Cocomys* relative to non-ctenodactyloid rodents? (2) What are the interrelationships among the Eocene ctenodactyloids? (3) What are the relationships of the Eocene forms to those of the Oligocene?

(1) *Cocomys* and other rodents. *Cocomys* shows an interesting combination of features. It shares with early ischyromyids the presumably primitive characters of being protrogomorphous, having molars with lophs only poorly developed, and possessing strong conules, especially metaconules. Added to this, it has the basic ctenodactyloid features of upper molar structure with the metaloph oriented toward the protocone and the hypocone a distinct cusp separated from the metaloph. In the lower molars there is a strongly developed hypoconulid on a posterior cingulum, which is separated by a notch from the hypoconid. Perhaps the most interesting feature of *Cocomys* is also the most enigmatic–the non-molariform $P\frac{4}{4}$.This is the feature that most convincingly links *Cocomys* with the post-Eocene ctenodactyloids. In the Oligocene and later ctenodactyloids the structure of $P\frac{4}{4}$ is based on that shown by *Cocomys,* and the more molariform $dP\frac{4}{4}$, first seen in *Cocomys,* also remains characteristie of the ctenodactyloids, although the permanent premolars may be strongly reduced or even lost in the adults. It is the structure of $P\frac{4}{4}$ that bears most strongly on the problem of the position of the ctenodactyloids relative to non-ctenodactyloids.

The described fossil record of the oldest known rodent, the Tiffanian *Paramys atavus,* consists of a few isolated teeth, one of which appears to be P^4 but is quite molariform with well developed paracone and metacone (McKenna, 1961:3). Wood (1962:139–147) considers P^4 of *Franimys amherstensis* to be primitive for rodents. This tooth, described as "not molariform, being the only known paramyid of which this is true" (Wood, 1962:142), has a lingual protocone and two closely spaced buccal cusps, paracone and metacone, of which the former is smaller. Wood hypothesizes (Wood, 1962: 146, 252–253) that "the ancestral P^4 would presumably have had a large internal protocone, an elongate external metacone, and low anterior and posterior cingula" and no paracone; P_4 of the "hypothetical ancestral paramyid" would lack a protoconid and have a small talonid.

More recently discovered evidence that may bear on the primitive condition for rodents comes from the Asian late Paleocene *Heomys,* a representative of the order Anagalida (Li, 1977) or the order Mixodontia (Sych, 1971; Hartenberger, 1980). Although *Heomys* itself is too late in time and too advanced in various morphological details, especially in degree of hypsodonty, to be in the ancestry of rodents, it seems likely that it belongs to the stock out of which the rodents originated. $P\frac{4}{4}$ in *Heomys* are non-molariform: P^4 has a single buccal cusp, and P_4 has the talonid narrower than the trigonid. With relatively little modification, the type of $P\frac{4}{4}$ found in *Cocomys* could be derived from that of *Heomys.* The upper molars, with hypocone present and metaconule well developed, have a pattern from which that of *Cocomys* could be derived.

If the primitive condition in rodents included non-molariform $P\frac{4}{4}$, as Wood suggested and as *Heomys* tends to corroborate, *Cocomys* would appear to have the most primitive premolars known for a rodent. In premolar structure at least, it would thus demonstrate a level more primitive than that of the known ischyromyids. It is difficult to know, from the incomplete fossil record, how far it is safe to extrapolate from that record. On the one hand, the evidence from *Heomys* and *Cocomys* suggests that primitive dental characters for rodents include non-molariform premolars, upper molars with a hypocone at least moderately well developed, and lower molars with a prominent posterior cingulum-hypoconulid. On the other hand, it must be remembered that the only known Paleocene rodent is still a North American ischyromyid, a group in which the premolars are more molariform than in the earliest ctenodactyloids and the molars are very simple, cuspate teeth. Hartenberger (1980:297–299) has suggested that the ctenodactylids (ctenodactyloids as used here) and ischyromyids are independently derived from a primitive rodent stock. Perhaps this was the case, although the evidence from *Heomys* and *Cocomys* could be used equally well to support derivation of the ischyromyids from a group with at least some ctenodactyloid characters.

The only Eocene rodent known from outside Asia with a non-molariform P^4 somewhat reminiscent of that in *Cocomys* is AMNH 12118, a maxilla with P^3–M^1 from the Bridger Formation of Wyoming (Dawson, 1962). Absence of other North American evidence precludes anything but tantalizing speculations on the significance of this similarity.

(2) Interrelationships among the Eocene ctenodactyloids. The Eocene ctenodactyloids of central and eastern Asia appear to fall into two morphologically distinct groups. In one, typified by *Cocomys* and *Tamquammys*, $P\frac{4}{4}$ are non-molariform, P^4 lacking the metacone and P_4 lacking a hypoconid and having a narrow talonid. The less well known *Tsinlingomys* belongs with this group. In the second group, typified by *Petrokozlovia* and *Yuomys*, P^4 is molariform with a metacone and P_4 has a hypoconid. *Advenimus* and (the probably synonymous) *Saykanomys* may be allied here. In Wood's review (1977) of the Ctenodactylidae, *Advenimus, Saykanomys*, and *Yuomys* were considered to be Eocene representatives of that family. *Cocomys* was unknown to Wood, *Tamquammys* was considered an indeterminate genus, and *Petrokozlovia* was not included. The more complete record now available documents a considerable central and eastern Asian radiation of ctenodactyloids during the Eocene and suggests also that at least two lines of descent had become established. The morphologies and histories of these lines lead us to establish them as two new ctenodactyloid families, the Cocomyidae and the Yuomyidae.

Family Cocomyidae

Type genus.—*Cocomys*, this paper.

Included genera.—*Cocomys, Tamquammys, Tsinlingomys.*

Geological range.—Early to middle Eocene.

Geographic distribution.—Kazakhstan, Inner Mongolia, China.

Diagnostic characters.—Ctenodactyloid rodents with skull protrogomorphous to hystricomorphous, mandible sciurognathous; dental formula, where known, $\frac{1}{1}, \frac{0}{0}, \frac{2}{1}, \frac{3}{3}$. Cheek teeth cuspate to lophate. $P\frac{4}{4}$ non-molariform, lacking metacone and hypoconid; dP^4 molariform where known; on upper molars protoconule present and metaconule well developed, on lower molars posterior arm of metaconid distinct, lophs of lower teeth transversely or posterolaterally oriented, when present.

Family Yuomyidae

Type genus.—*Yuomys* Li (1975)

Included genera.—*Petrokozlovia, Yuomys. Advenimus* and *Saykanomys* (probably a synonym of *Advenimus*) are tentatively referred.

Geological range.—Late Eocene. *Advenimus* from late early or early middle Eocene.

Geographic distribution.—Kazakhstan, Mongolia, Inner Mongolia, China.

Diagnostic characters.—Ctenodactyloid rodents with skull hystricomorphous, mandible sciurognathous; dental formula, $\frac{1}{1}, \frac{0}{0}, \frac{2}{1}, \frac{3}{3}$. Cheek teeth cuspate to lophate. $P\frac{4}{4}$ sub-molariform, with metacone and hypoconid present; on upper molars protoconule present, metaconule especially well developed and persistent; posterior arm of metaconid distinct; lophs of lower teeth transversely oriented, where present.

Discussion.—The most important distinctions between the Cocomyidae and Yuomyidae are in the structure of $P\frac{4}{4}$. The Cocomyidae, as discussed above, are the more primitive in these teeth, retaining their non-molariform nature, although dP^4 has become molariform (and it may be predicted that dP_4 would be also, with hypoconid present). The earliest cocomyids, also the geologically oldest ctenodactyloids, have a protrogomorphous skull, with the infraorbital foramen approximately the same relative size as in contemporary sciuravids and having no sign of transmittal of masseter muscle. In the middle Eocene the known cocomyids are hystricomorphous, as are the yuomyids. If *Advenimus* is a yuomyid, molarization of $P\frac{4}{4}$ characterizing the family had taken place by the late early Eocene or early middle Eocene. *Petrokozlovia* and *Yuomys* somewhat parallel the cylindrodontids in their strongly lophate teeth.

The rodents *Birbalomys* and *Metkamys* from the middle Eocene of India (Sahni and Khare, 1973; Sahni and Srivastava, 1976, 1977) and the rodents referred to the family Chapattamyidae from the middle Eocene of Pakistan (Hussain and others, 1978) are now under re-study by Sahni and Hartenberger (personal communication, April 1981). These rodents are known by many isolated teeth and a few more complete specimens. They are characterized by molars that increase in size toward the posterior, distinct molar hypocone, conules well developed, crest from the metacone to or toward the protocone, complete metalophulid I, and well developed hypoconulid. These are characters basic to the ctenodactyloids. These Eocene rodents of India and Pakistan are further characterized by P_4 with a well developed hypoconid and a wider talonid than trigonid. Their lower molars have a hypolophid that curves anterobuccally and contacts an anterolingual ridge from the hypoconid. Of the central and eastern Asian ctenodactyloids, *Advenimus* and *Saykanomys* (reference by Hussain and others, 1978, of several species from Pakistan to *Saykanomys* is here considered incorrect) are closest to those from the Indian region. However, *Advenimus* and *Saykanomys* have a different morphology of the hypolophid and many of their similarities to the Indian species are in primitive features. Studies now underway by Sahni and Hartenberger on the Indian fossils and by de Bruijn (personal communication, October 1981) on newly discovered early Eocene rodents in Pakistan should clarify the nature of the affinities among these Asian ctenodactyloids.

The presently known Eocene rodent record of Asia shows a dominance of ctenodactyloids, somewhat similar to the Eocene dominance of theridomorphs in Europe. Ischyromyids are present, though apparently not abundant, in the Eocene of Asia, but theridomorphs and sciuravids are absent.

(3) Relationships between the eastern and central Asian Eocene ctenodactyloids and those of the Oligocene. Revision of the post-Eocene ctenodactyloid rodents is outside the scope of this paper, but at least some suggestions of the affinities between Eocene and later forms may be ventured. Six genera of Oligocene ctenodactylids have been reported from eastern and central Asia, *Tataromys, Karakoromys, Leptotataromys, Yindirtemys, Woodomys,* and *Terrarboreus.* Of these *Leptotataromys* and *Yindirtemys* are too poorly known to figure in the discussion. Better known are *Tataromys* and *Karakoromys* (Matthew and Granger, 1923:5–7; Bohlin, 1946). These genera are hystricomorphous sciurognaths, have a jaw with reduced coronoid process and masseteric fossa bounded by strong ventral crest, dental formula $\frac{1}{1}$, $\frac{0}{0}$, $\frac{1}{1}$, $\frac{3}{3}$, non-molariform $P\frac{4}{4}$, and strongly lophate molars, which increase in size to the posterior and have a prominent posterior lophid involving the hypoconulid. The strongest evidence on affinities of these Oligocene genera to those of the Eocene is found in the structure of $P\frac{4}{4}$, which indicates that the Cocomyidae are allied to this group. *Woodomys,* known from lower jaws and teeth from the middle Oligocene of Mongolia and Kazakhstan, and *Terrarboreus,* known by one maxilla from the middle Oligocene of Kazakhstan (Shevyreva, 1971*b*) are more difficult to place with the ctenodactylids. *Terrarboreus,* originally described as a sciuravid, was referred by Wood (1977:126–127) to the Ctenodactylidae on the basis of its hystricomorphy, premolar reduction, and molar pattern. The molars share some probably primitive features with the Eocene ctenodactyloids. P^4, broken in the only known specimen, appears to have a hypocone and be well developed buccally, suggesting that, if a ctenodactyloid, *Terrarboreus* is closer to the Yuomyidae than to the Cocomyidae. *Woodomys* is more clearly a ctenodactyloid, with a narrow talonid of P_4, which does seem to have a small hypoconid, and a development of the molars that is somewhat more primitive than in *Tataromys* and *Karakoromys.* Wood (1977:127) suggested that *Terrarboreus* may be the maxilla of *Woodomys,* but this association is far from established. Until *Woodomys* and *Terrarboreus* are better described, it may be best to regard them as ctenodactyloids *incertae sedis.*

Following Bohlin's (1946) demonstration of the relationships between *Tataromys, Karakoromys,* and *Sayimys* of China and Mongolia and the Recent Ctenodactylidae, the post-Oligocene history of the family became more clear. Neogene ctenodactylids have been recognized in India (Black, 1972), North Africa (Lavocat, 1961; Jaeger, 1971; Robinson and Black, 1973), Sicily (Bohlin, 1946; Jaeger, 1971), and Sardinia (de Bruijn and Rümke, 1974). The family also includes the extant North African genera

Ctenodactylus, Pectinator, Massoutiera, and *Felovia,* and may be distinguished as follows:

Family Ctenodactylidae Zittel (1893)

Included genera.—Karakoromys, Tataromys, Leptotataromys, Yindirtemys, Sayimys, Metasayimys, Africanomys, Testouromys, Sardomys, Pireddamys, Irhoudia, Pellegrinia, Pectinator, Massoutiera, Ctenodactylus, Felovia.

Geologic range.—Oligocene to Recent.

Geographic distribution.—Asia (Oligocene to Pliocene), northern Africa (Miocene to Recent), Sardinia (Miocene), Sicily (Pleistocene).

Diagnostic characters.—Rodents with skull hystricomorphous, jaw sciurognathous; lower jaw with coronoid process from reduced to nearly absent, condyle not high, strong lateral crest forms ventral border of insertion of masseter medialis. Incisor enamel multiserial where known. Dental formula $\frac{1}{1}$, $\frac{0}{0}$, $\frac{2\text{–}1}{1\text{–}?0}$, $\frac{3}{3}$. $P\frac{4}{4}$ non-molariform, smaller than molars, and may be lost early in life, $dP\frac{4}{4}$ more molariform; molars increase in size to posterior; upper molar pattern based on quadrate arrangement with hypocone, become bilobate; lower molars based on arrangement with large hypoconulid lobe, become tri- or bilobate; brachydont to hypsodont.

The superfamily Ctenodactyloidea Simpson (1945) can now be seen to be a very old group that underwent its initial radiation in Asia during the Eocene. Characters of the superfamily are as follows: skull protrogomorphous in the oldest known form, *Cocomys,* but hystricomorphous in all others; jaw sciurognathous, showing modifications in post-Eocene forms toward reduction of coronoid process and development of strong ridge of masseteric fossa; incisor enamel where known multiserial in post-Eocene forms, pauciserial in Eocene forms (Sahni, 1980); dental formula $\frac{1}{1}$, $\frac{0}{0}$, $\frac{2\text{–}1}{1\text{–}?0}$, $\frac{3}{3}$; deciduous teeth relatively well developed and more molariform than $P\frac{4}{4}$; molars increase in size from $M\frac{1}{1}$ to $M\frac{3}{3}$; upper molars based on plan with prominent conules, hypocone present but not joined to metaloph, which is oriented toward protocone, and lacking a mesoloph, become lophate, and finally bilobate in Recent forms; lower molars based on plan without mesolophid, with emphasis on posterolophid and hypoconulid, become lophate and finally bilobate or trilobate.

Two distinct lines of ctenodactyloids, here recognized as the two families Cocomyidae and Yuomyidae, are present in the Eocene. The major distinctions between these families are in the structure of $P\frac{4}{4}$. The Cocomyidae have non-molariform $P\frac{4}{4}$, which appears to be the primitive rodent condition, and which characterizes as well the Ctenodactylidae, probable descendants of the Cocomyidae. In the Yuomyidae $P\frac{4}{4}$ are sub-molariform, and this family also developed lophate cheek teeth reminiscent of those in cylindrodontids. The yuomyids appear to have left no descendants past the Eocene, unless the affinities of the middle Oligocene *Terrarboreus* are here.

Following their Eocene dominance in Asia, the ctenodactyloids persisted into the Oligocene and early Miocene in eastern Asia. Their range became restricted more and more to the south and west, and by the late Miocene they were apparently gone in eastern Asia but still occurred in India and had extended into the Mediterranean region and northern Africa. Their present distribution, limited to northern Africa, and ecological role in the African rodent faunas contrasts strongly with their Eocene radiation in Asia.

LITERATURE CITED

Black, C. C. 1972. Review of fossil rodents from the Neogene Siwalik beds of India and Pakistan. Palaeont., 15:238–266.

Bohlin, B. 1946. The fossil mammals from the Tertiary deposit of Taben-buluk. Part 2. Simplicidentata, Carnivora, Artiodactyla, Perissodactyla, and Primates. Palaeont. Sinica, new ser. C, 8b:1–259.

Bruijn, H. de, and C. Rümke. 1974. On a peculiar mammalian association from the Miocene of Oschiri (Sardinia). Proc. Kon. Nederl. Akad. Wet., ser. B, 77(1):46–79.

Bugge, J. 1974. The cephalic arterial system in insectivores, primates, rodents and lagomorphs, with special reference to the systematic classification. Acta Anat., 87(suppl. 62):1–160.

Dawson, M. R. 1962. A sciuravid rodent from the middle Eocene of Wyoming. Amer. Mus. Novit., 2075:1–5.

———. 1964. Late Eocene rodents (Mammalia) from Inner Mongolia. Amer. Mus. Novit., 2191:1–15.

———. 1977. Late Eocene rodent radiations: North America, Europe and Asia. Geobios, Mem. Spec., 1:195–209.

Gregorio, A. de. 1887. Intorno a un deposito de roditori e di carnivori sulla vetta di Monte Pellagrino con uno schizzo sincronografico del calcare postpliocenico della vallata di Palermo. Mem. Atti Soc. toscana, Sci. Nat., 8:217–253.

Guthrie, D. A. 1963. The carotid circulation in the Rodentia. Bull. Mus. Comp. Zool., Harvard Univ., 128(10):455–481.

Hartenberger, J.-L. 1980. Données et hypothèses sur la radiation initiale des rongeurs. Palaeovertebrata, Mem. Jubil. R. Lavocat:285–301.

Hinton, M. A. C. 1933. Diagnoses of new genera and species of rodents from Indian Tertiary deposits. Ann. Mag. Nat. Hist., ser. 10, 12 (72):620–622.

Hussain, S. T., H. de Bruijn, and J. M. Leinders. 1978. Middle Eocene rodents from the Kala Chitta Range (Punjab, Pakistan). Proc. Kon. Nederl. Akad. Wet., ser. B, 81(1):74–112.

Jaeger, J.-J. 1971. Un cténodactylidé (Mammalia, Rodentia) nouveau, *Irhoudia bohlini* n.g., n.sp., du Pléistocene inférieur du Maroc. Rapports avec les formes actuelles et fossiles. Notes Serv. géol. Maroc, 31(237):113–140.

Lavocat, R. 1961. Le gisement de vertébrés Miocènes de Beni Mellal (Maroc). Étude systématique de la faune de mammifères. Notes et Mém. Serv. Géol. Maroc, pp. 29–94.

Li, C. 1963. [Paramyids and sciuravids from North China]. Vert. Palasiatica, 7(2):151–160.

———. 1975. [*Yuomys*, a new ischyromyoid rodent genus from the Upper Eocene of North China]. Vert. Palasiatica, 13(1): 58–70.

———. 1977. [Paleocene eurymyloids (Anagalida, Mammalia) of Qianshan, Anhui]. Vert. Palasiatica, 15(2):103–118.

Li, C., C. Chiu, D. Yan, and S. Hsieh. 1979. [Notes on some Early Eocene mammalian fossils of Hengtung, Hunan]. Vert. Palasiatica, 17(1):71–80.

Luckett, W. P. 1971. The development of the chorio-allantoic placenta of the African scaly-tailed squirrels (Family Anomaluridae). Amer. J. Anat., 130:159–178.

Matthew, W. D., and W. Granger. 1923. Nine new rodents from the Oligocene of Mongolia. Amer. Mus. Novit., 102: 1–10.

McKenna, M. C. 1961. A note on the origin of rodents. Amer. Mus. Novit., 2037:1–5.

Qi, T. 1979. [A general account of the Early Tertiary mammalian faunas of Shara Murun area, Inner Mongolia]. Second Cong. Strat. China, Peking, pp. 1–9.

Robinson, P., and C. C. Black. 1973. A small Miocene faunule from near Testour, Beja Gouvernorat, Tunisia. Ann. Mines Geol., Tunis, 26:445–449.

Sahni, A. 1980. SEM studies of Eocene and Siwalik rodent enamels. Geoscience J., 1(2):21–30.

Sahni, A., and S. K. Khare. 1973. Additional Eocene mammals from the Subathu Formation of Jammu and Kashmir. J. Palaeont. Soc. India, 17:31–49.

Sahni, A., and V. C. Srivastava. 1976. Eocene rodents and associated reptiles from the Subathu Formation of northwestern India. J. Paleont., 50(5):922–928.

Sahni, A., and M. C. Srivastava. 1977. Eocene rodents of India: their palaeobiogeographic significance. Geobios, Mem. Spec., 1:87–95.

Shevyreva, N. S. 1971*a*. [The first find of Eocene rodents in the U.S.S.R.]. Bull. Acad. Sci. Georgian S.S.R., 61(3):745–747.

———. 1971*b*. [New middle Oligocene rodents from Kazakhstan and Mongolia]. Acad. Sci. U.S.S.R., Trans. Palaeont. Inst., 130:70–86.

———. 1972. [New rodents in the Paleogene of Mongolia and Kazakhstan]. Palaeont. J., 3:134–145.

———. 1976. [Paleogene rodents of Asia]. Acad. Sci. U.S.S.R., Trans. Palaeont. Inst., 158:1–115.

Simpson, G. G. 1945. The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist., 85: 1–350.

Sych, L. 1971. Mixodontia, a new order of mammals from the Paleocene of Mongolia. Palaeont. Polonica, 25:147–158.

Teilhard de Chardin, P. 1926. Mammifères Tertiaires de Chine et de Mongolie. Ann. Paléont., 15:1–51.

Wood, A. E. 1937. Fossil rodents from the Siwalik beds of India. Amer. J. Sci., ser. 5, 34:64–76.

———. 1962. The early Tertiary rodents of the family Paramyidae. Trans. Amer. Philos. Soc., new ser., 52(1):1–261.

———. 1977. The evolution of the rodent family Ctenodactylidae. J. Palaeont. Soc. India, 20:120–137.

Xu, Y., D. Yan, S. Zhou, S. Han, and Y. Zhang. 1979. The subdivision of the Red Beds of South China. Pp. 416–432 *in* The Mesozoic and Cenozoic Red Beds of South China, Science Press, Beijing, 432 pp. (in Chinese).

Zittel, K. A. von. 1893. Handbuch der Paläontologie. Abt. 1. Paläozoologie. Bd. IX, Vertebrata (Mammalia). R. Oldenbourg, Munich, 799 pp.

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HYSTRICOGNATHY IN THE NORTH AMERICAN OLIGOCENE RODENT *CYLINDRODON* AND THE ORIGIN OF THE CAVIOMORPHA

Albert E. Wood

ABSTRACT

The historic use of the masseter muscle and of the shape and attachment of the angular process of the mandible in the classification of the Rodentia is reviewed. At least two types of modification of the masseter (sciuromorphy and hystricomorthy) have evolved independently, as parallelisms, a considerable number of times, as is also true of the patterns of the cheek teeth. It is therefore important to determine whether hystricognathy has arisen only once or more than once within the order. Incipient hystricognathy is present in a number of North American Eocene rodents of the Infraorder Franimorpha. There is no current evidence as to whether all fully hystricognathous rodents are descended from a single subhystricognathous franimorph; whether the various groups of late Tertiary and living hystricognaths are descended from several such franimorphs; or whether hystricognathy evolved entirely as parallelisms, the modern groups of hystricognaths being descended from several sciurognathous ancestors.

Two specimens of the North American Oligocene cylindrodont rodent *Cylindrodon* are described that were clearly at least subhystricognathous. The insertions of the various jaw muscles on the mandible are identified.

Because the Paleocene *Franimys* was subhystricognathous, it follows that, if hystricognathy arose from sciurognathy only once among rodents, the middle Eocene cylindrodont *Mysops* must also have been at least subhystricognathous. This genus, known to have been present in Middle America, the area whence the ancestors of the South American Caviomorpha must have come if they were New World forms, is the only middle Eocene genus known from any part of the world that had the morphological capabilities to have been a caviomorph ancestor.

INTRODUCTION

Since the early part of the last century (Waterhouse, 1839), the modifications of the masseter muscle, as exemplified by the conditions in *Sciurus, Rattus,* and *Hystrix,* have been considered to be of importance in the higher-level classification of the rodents. These ideas were formalized (Brandt, 1855) in the familiar Suborders Sciuromorpha, Myomorpha and Hystricomorpha. Among Recent rodents, the African Bathyergidae and the North American *Aplodontia* do not fit into this classification, but were traditionally included in the Hystricomorpha and Sciuromorpha, respectively. Tullberg (1899) noted that there were two types of angular process among the rodents. In one, sciurognathous, the angle arises from the ventral side of the alveolus of the lower incisor, and is in the same vertical plane as this alveolus. In the other, hystricognathous, the angular process arises from the lateral side of the mandible, lateral to the incisive alveolus, and thus lateral to the vertical plane that includes the alveolus. Tullberg used this character, as well as the structure of the masseter muscle, in his classification, dividing the Rodentia (as the Suborder Simplicidentati) into the Tribes Sciurognathi and Hystricognathi, the former including the Subtribes Sciuromorphi and Myomorphi and the latter the Subtribes Hystricomorphi and Bathyergomorphi. However, in addition to *Aplodontia,* this classification did not provide a suitable place for the sciurognathous but hystricomorphous Dipodoidea, Anomaluridae, Ctenodactylidae, and Pedetidae, or for the Eocene to Oligocene European rodents now included in the Theridomyoidea (Theridomyidae and Pseudosciuridae).

None of the classifications of the nineteenth century gave much consideration to fossil rodents. This is likewise true of that of Ellerman (1940–1941). The first real effort to do so was the classification of Miller and Gidley (1918), which attempted to arrive at a classification of the rodents that was phylogenetically reasonable. Most later classifications of all or part of the order have tried to work toward the same goals that Miller and Gidley did, with varying success. Among such classifications are those of Simpson (1945), Wilson (1949*a*:77), Schaub (1953, 1958), Thaler (1966), Lavocat (1973, 1976), Wood (1937, 1955, 1959*a*, 1959*b*, 1965, 1974*c*, 1975, 1980*a*) and Patterson and Wood (1982). Lavocat, Wood, and Patterson and Wood have returned to the basic division of the Rodentia into two suborders, the Sciurognathi and Hystricognathi, as proposed by Tullberg (1899).

Increase in our knowledge of Eocene rodents has demonstrated that most of these, as well as *Aplodontia,* differed from the vast majority of Recent rodents in that the origin of the masseter muscle remained on the zygoma, and the muscle had not begun to migrate onto the snout or to modify the infraorbital foramen. This primitive condition of the masseter has been called protrogomorphy, and the rodents that showed this condition were united (Wood, 1937:160) as an ancestral Suborder Protrogomorpha.

Wilson (1949*a*:153–157) raised questions as to whether any of the subordinal groups as then recognized were natural, or whether there should be extensive shifting of families and superfamilies among the suborders. Subsequent work has shown that the sciuromorphous condition of the Sciuridae (Black, 1963:127) and Castoroidea (Castoridae + Eutypomyidae) (Wood, 1974*a*:87, 95–96) must have evolved independently from protrogomorphous ancestors, as was likewise true of the sciuromorphous ischyromyid genus *Titanotheriomys* (Wood, 1976:266). Wilson (1949*a*:113; 1949*b*:42–48) demonstrated that the sciuromorphous Eomyidae, Heteromyidae and Geomyidae were clearly related, and his work showed enough similarities between this group and what were then included in the Myomorpha to suggest (1949*a*:154) that perhaps they should all be united in a single suborder. Wood (1955:168, 176–179) accepted this idea, and placed the Eomyidae, Heteromyidae and Geomyidae (as a Superfamily Geomyoidea) in the Suborder Myomorpha. Thus, the consensus would seem to be that sciuromorphy arose at least four times, independently, as parallelisms, in the Sciuridae, Castoroidea, *Titanotheriomys,* and the Geomyoidea.

The importance of hystricomorphy as a basic diagnostic character has been extensively argued. But, whatever the relationships or lack thereof between the South American Caviomorpha and the Old World Hystricomorpha and Bathyergomorpha, it seems certain that hystricomorphy in the Theridomyoidea was of independent origin (Wood, 1974*b*: 30–31, Fig. 4). There is no possible interpretation of the relationships of the various rodent groups involved that could explain the hystricomorphy of the dipodoids as anything but an independent development. The Ctenodactylidae seem clearly to have evolved from Eocene north Asiatic ancestors and to have had nothing to do with the origin of either the Hystricomorpha or of the Bathyergomorpha (Wood, 1977*a*:122–126, 133), Hussein et al. (1978) to the contrary notwithstanding. Nothing is currently known of the origins of either the Anomaluridae or Pedetidae (both first appear in the early Miocene of Africa), but it seems obvious, to me at least, that they were not related to the African Thryonomyoidea. A number of North (and Middle) American Eocene rodents were hystricomorphous, including (at least) *Protoptychus* (Wahlert, 1973:7) and *Prolapsus* (Wood, 1977*b*:104), and possibly *Rapamys* (Wood, 1962:148, Fig. 52A).

Although it is possible that this hystricomorphy of some or all of the known New World Eocene hystricognathous forms evolved in common with that of the ancestors of the Caviomorpha (Wood, 1973:30–33; 1974*b*:31–33; 1975:78; 1977*b*:104–105; 1981:86; Patterson and Wood, 1982:449–450), these Eocene forms surely were not directly ancestral to any of the Old World hystricomorphous groups.

Therefore, hystricomorphy must have developed, independently, in at least five groups of rodents: the New World Eocene franimorphs; the European Eocene-Oligocene Theridomyoidea; the Dipodoidea; the north Asiatic Eocene Ctenodactylidae; and the Old World hystricognaths. Hystricomorphy may have arisen independently several additional times. For example, we have no information as to whether all the New World hystricomorphous franimorphs stem from a common source, or whether hystricomorphy arose independently two or more times within the group. Unless the Anomaluridae were derived from the Theridomyoidea, they must represent an independent origin of hystricomorphy. Nothing is known that suggests to me that the Pedetidae are related to any other hystricomorphous stock, so they may also have evolved hystricomorphy independently. It seems clear (Wood and Patterson, 1970:632–633; Wood, 1974*b*:38; Patterson and Wood, 1982:518–519) that the largely African Thryonomyoidea are too specialized, particularly in the retention of dP_4^4, to have given rise to the Hystricidae, as Lavocat (1973:153–158) believed they did. Although it is possible that the Hystricidae gave rise to the Thryonomyoidea (Patterson and Wood, 1982:518–519), there is no present evidence that they did, and the two groups may well have had independent origins from incipiently hystricognathous, but still protrogomorphous, ancestors, in which case this would represent another origin of hystricomorphy. Hystricomorphy is generally absent in the Bathyergidae, although it was well developed in *Bathyergoides* (Lavocat, 1973: Pl. 7, Fig. 4) and is technically present in *Cryptomys coecutiens*

(Tullberg, 1899: Pl. 2, Fig. 17). In view of the complete absence of hystricomorphy in the north Asiatic Oligocene Tsaganomyidae (probably closely related to the Bathyergidae), the bathyergomorphs would also seem to have acquired their limited amount of hystricomorphy independently, and perhaps even twice. Thus, it would seem that hystricomorphy could have evolved at least 9 or 10 times, in both related and unrelated stocks of rodents.

Although this is extensive parallelism, from what we know of parallelism in other features among the Rodentia, this should not be surprising.

It has been clear for a long time (Engesser, 1979: 41–42; Fahlbusch, 1970: much of paper, but especially pp. 98–102; Lavocat, 1951; 1954:127; 1955: 634; Patterson and Wood, 1982:450, 491–492; Vianey-Liaud, 1972; Wood, 1935:249; 1936; 1947: 156–161; 1950:90–97; 1965:122–124; 1974*b*:38–41; 1974*c*:977; 1975:76–77; 1977*a*:133–136; 1980*b*: 267–268; Wood and Patterson, 1970:631) that rodents have demonstrated a vast amount of parallelism in all features and at all levels, especially in the development of cheek-tooth patterns. Schaub (1953, 1958:691–694; see Wood, 1965:124) tried to base the classification of the order on cheek-tooth structure, but, in spite of his encyclopedic knowledge of the order, his conclusions have been generally disregarded (for a recent exception, see Lavocat, 1976:84–86), and his classification ignored. The evidence for parallelism in rodent cheek-tooth patterns was just too overwhelming.

It therefore becomes of major importance to determine whether hystricognathy originated only once, or whether it, too, developed independently two or more times within the Rodentia.

Lavocat's classification (1973, 1976) accepts implicitly, and that of Patterson and Wood (1982:476) explicitly, the postulate that hystricognathy is a valid basis for isolating one group of rodents as the Suborder Hystricognathi, *because hystricognathy is assumed to have originated only once in the evolution of the rodents,* and, therefore, all hystricognathous forms are descended from a single hystricognathous ancestor. However, both Hoffstetter (1973:159, 161) and Patterson and Wood (1982: 476) recognize the possibility that hystricognathy may have evolved as parallelisms in two or more distinct stocks. Such an event would make the subordinal classification of the rodents exceedingly difficult, because there would then be no feature that could be used as a morphological criterion automatically to subdivide the Rodentia.

However, one possibility that needs to be investigated further is that there may have been an extensive Eocene stock, largely protrogomorphous, that was incipiently hystricognathous (the Infraorder Franimorpha of Wood, 1975:78–79), and that full hystricognathy, as well as hystricomorphy, developed independently from such an ancestral stock, as parallelisms, in several lines of Oligocene and later (as well as Eocene) rodents. There is, at present, little or no evidence permitting one to decide whether: (1) all fully hystricognathous rodents arose from a single subhystricognathous franimorph; (2) a number of different subhystricognathous franimorphs gave rise to, e.g., the Caviomorpha, Bathyergomorpha, and Hystricomorpha (if the last are a monophyletic group); or (3) the modern hystricognaths had several distinct sciurognathous ancestors, hystricognathy having evolved completely as parallelisms. I personally favor the second possibility. Whatever the evolutionary sequences, hystricognathy presumably resulted from selection for the elongation and more anteroposterior alignment of the *Pterygoideus internus* (Woods, 1972:131). Woods believed that this was related to the development of propalinal chewing. It seems much more probable to me that the modification of the *Pterygoideus internus* was one of several changes that were the result of selection for increased gnawing ability, and that propalinal chewing was a secondary result, permitted by the changes in the jaw musculature.

In general, hystricognaths are Oligocene or later, most students having, at least implicitly, considered Eocene rodents to have been sciurognathous. Some years ago, Landry (1957:82) noted that the North American middle Eocene rodent *Reithroparamys* possessed an incipiently hystricognathous angle of the lower jaw. I observed (1962:117) that there were a number of other Eocene rodents, and even one from the latest Paleocene (Wood, 1974*a*:16–17), included by me in the Reithroparamyinae, that also possessed this type of angular process. I considered this one of the fundamental diagnostic characters of the subfamily. Hystricognathous angular processes have since been observed in other Eocene rodents, including ones from West Texas (Wood, 1972; 1973:22, 27–29) and Mexico (Black and Stephens, 1973:2–4), and possibly, *Protoptychus* (Wahlert, 1973:14). These are, to date, the only Eocene rodents described from any part of the world that have been shown to have been hystricognathous or incipiently hystricognathous.

Because these rodents are all more primitive than any hitherto recognized Oligocene or later hystricognaths (the South American Oligocene and later Caviomorpha, and the Old World Oligocene and later Hystricomorpha and Bathyergomorpha—for the classification of the rodent Suborder Histricognathi, see Patterson and Wood, 1982:509–523), I (1975: 78–79) grouped them in a new, ancestral, infraorder of the Suborder Hystricognathi, the Franimorpha, including the Reithroparamyinae, the Protoptychidae, and the genera (of uncertain familial allocation) *Guanajuatomys* and *Prolapsus.* This classification left the Reithroparamyinae in the Family Paramyidae, along with several sciurognathous subfamilies. This arrangement seemed (and still seems) entirely reasonable to me; the Reithroparamyinae had diverged from the other paramyids in characters that I now consider of subordinal significance, but had not yet diverged in characters that I consider of familial importance (Wood, 1980*b*: 265–266). If one considers that a classification should be indicative of the evolution that actually occurred, there should be no objection to such an arrangement. If one feels (as I believe to be the case with many contemporary taxonomists) that a classification should be a rigid filing system that could be entrusted to a computer, then such an arrangement becomes anathema.

The late Bryan Patterson argued, in connection with our study of the early Oligocene rodents of Bolivia (Patterson and Wood, 1982), that this arrangement would not be acceptable to most taxonomists, and that we should separate the Reithroparamyinae from the Paramyidae at the familial level as well as at that of the suborder. I reluctantly agreed that this was probably the best solution to follow, and we have, therefore, recognized the Reithroparamyidae as a distinct family of the Infraorder Franimorpha within the Suborder Hystricognathi (Patterson and Wood, 1982).

As pointed out elsewhere (Wood, 1980*b*:270; Patterson and Wood, 1982:476), hystricognathy could not have arisen, *de novo,* fully developed, but must have evolved in stages. Furthermore, the selection was probably not for hystricognathy, but rather for the more anteroposterior alignment and increased length of the *Pterygoideus internus* (Woods, 1972: 131; Wood, 1980*b*:269–270; 1981:80–81; Patterson and Wood, 1982:476–477), a muscle that arises from the pterygoid fossa, just behind the cheek teeth, and that inserts on the inner surface of the angular process (Fig. 1D–F). This muscle, although less important to rodents than the masseter, is nevertheless a very important factor in the anteroposterior motion of the lower jaw in gnawing, especially among the hystricognaths.

It is therefore quite interesting, and presumably significant, that there have been no Eocene hystricognaths as yet described from any part of the Old World. Lavocat (1973:163) referred to an Eocene rodent from Pakistan, presumably ancestral to the African Oligocene Thryonomyoidea (Phiomyidae of Wood, 1968; Phiomorpha of Lavocat, 1973:20; 1976). This specimen was referred to by Wood (1977*b*:104), on the authority of Lavocat. This was apparently one of the forms since described by Hussain et al. (1978) as a member of their Chapattimyidae, a group that they considered ancestral not only to the Thryonomyoidea and through them to the Caviomorpha, but also, surprisingly, to the North American Middle Eocene to Oligocene Cylindrodontidae. No lower jaws of any of the Pakistani rodents referred to the Chapattimyidae appear to be known. The lower jaws of all the northern Asiatic genera placed in this family by Hussain et al. (but placed in the Ctenodactylidae by Wood, 1977*a*) were sciurognathous; the cheek teeth of the Pakistan "chapattimyds" look much more like those of ctenodactylids than like those of thryonomyoids; there is no indication in any "chapattimyid" of any tendency toward retention of dm^4_4 as is true of all thryonomyoids; and the incisor enamel (contrary to the statement by Hussain et al., 1978:104) is a diagrammatic example of the primitive type of rodent enamel, the pauciserial one (Wahlert, 1968:Fig. 1c; Korvenkontio, 1934:Pl. 34, Figs. 1–2). Therefore, these Pakistani rodents must at present be considered to be members of the Sciurognathi, and seem to have been either ctenodactyloids or, more probably, ctenodactylids, with no relationship to the cylindrodonts or to the thryonomyoids.

Some years ago (Wood, 1974*a*:53), I was impressed by a number of similarities between the tooth pattern of certain early Oligocene cylindrodonts (Subfamily Jaywilsonomyinae) of Mexico and that of the Deseadan caviomorphs of South America, but stressed that this was merely an example of parallelism rather than an indication of relationship, because, at that time, I believed the cylindrodonts to have been sciurognathous.

Recently, however, I came upon a specimen of the early Oligocene cylindrodont *Cylindrodon fontis* in the collections of the American Museum of Natural History (A.M.N.H. no. 94501), in which both lower jaws, essentially complete, were preserved articulated with the skull. A ventral view of the lower jaw clearly shows that the angular process is lateral to the incisive alveolus and that it arises from the lateral wall of the alveolus (Wood, 1981:Fig. 2d), conditions typical of hystricognathy. These are apparently the first North American cylindrodont jaws to be reported in which all or nearly all of the angular processes are preserved.

However, once it is recognized that the cylindrodonts might have been hystricognathous, illustrations of other, more fragmentary jaws suggest that the angle arose, in various members of this family, from the lateral surface of the alveolus, and that the ventral margin of the horizontal ramus passes mesiad of the beginnings of the angular process. Such figures include: Black, 1965:Fig. 2b (*Pseudocylindrodon neglectus*); Burke, 1935:Figs. 1–2 (*Pseudocylindrodon neglectus* and *Cylindrodon fontis*); Matthew and Granger, 1925:Fig. 8 (*Ardynomys olseni*); Shevyreva, 1976:Fig. 8 d–e (*Morosomys silentii*); Wood, 1937:Pl. 24, Fig. 1 (*Cylindrodon fontis*); 1970:Figs. 1a, 2a (*Ardynomys olseni*); 1974*a*: Figs. 14d (*Cylindrodon fontis*), 15c (*Pseudocylindrodon neglectus*), 19a (*Pseudocylindrodon* cf. *texanus*) and 24c and 25i (*Jaywilsonomys pintoensis*). Students had not expected these forms to have been hystricognathous, and therefore had not recognized the condition, particularly since there usually had been extensive breakage of the angular processes. The lateral views of the jaws of these forms (the only medial views published were those of *Ardynomys olseni*: Matthew and Granger, 1925:Fig. 8; Wood, 1970:Fig. 2a; and Shevyreva, 1976:Fig. 9b; and of *Morosomys silentii*: Shevyreva, 1976, Fig. 8e) show almost as much indication of hystricognathy as does the corresponding view of the undoubted hystricognath *Prolapsus* from the Big Bend area of Texas (Wood, 1973:Fig. 5a). It should be pointed out, however, that the jaw of *Cylindrodon* is not fully hystricognathous because there is no suggestion of the expansion of the *Masseter superficialis, pars reflexa* onto the medial side of the bone. This expansion, presumably unrelated to the lengthening of the *Pterygoideus internus,* is characteristic of fully hystricognathous rodents.

DESCRIPTION

Two lower jaws of *Cylindrodon fontis* are of special interest. Both rami of the lower jaw of A.M.N.H. no. 94501 (collected by J. R. Hough, near Cameron Springs, Wyoming, in 1959) were in place, missing the anterior portion including the symphysis. The premaxillae are also missing. At least nine vertebrae (the first postcranial material of *Cylindrodon* to be reported) are also present, at least in part articulated.

In ventral (Fig. 1A) or posterior (Fig. 1B) view, the entire ascending ramus and angular process lie lateral to the course of the lower incisor. This is almost identical to the conditions in *Cyclomylus lohensis* figured by Shevyreva (1976:Fig. 12z). The masseteric crest (Woods, 1972:Fig. 1a), marking the insertion of the *Masseter lateralis profundus* (Woods, 1972:125) begins high on the mandible, beneath the anterior part of M_2 immediately below the scar for the insertion of the tendon of the *Masseter medialis anterior* (Fig. 1C), and passes the ventral margin of the horizontal ramus at the level of the middle of M_3. The incisor (Fig. 1A) ends just behind the rear of M_3.

In mesial (Fig. 1D) or posterior (Fig. 1B) view, the prominent inflected angle can be seen, folded inward to make an exceedingly deep cavity. It has proven impossible to remove all the matrix from this area (Fig. 1B), but it seems certain that, at most, there is only a small nutritive foramen in its bottom. The median wall of this fossa, the inflected portion of the angle, lies in the plane of the incisive alveolus. Anterior and dorsal to this cavity is a shallower pit that lies within the area of insertion of the *Masseter superficialis, pars reflexa* (Woods, 1972:123–124, Fig. 3b). The ventral and medial surfaces of the inflected angle were the area of insertion of the main portion of the *Masseter superficialis* (Woods, 1972: 123). The dorsal margin of the inflected angle is continued forward, upward and then backward, as a well-marked crest, that fades out below and anterior to the condyle and that separates the main body of the mandible from the angular process. This crest marks the anterior limit of the insertion of the *Masseter superficialis, pars reflexa* (Woods, 1972: 123–124). The mandibular foramen leads into the jaw about half way between the posterior ends of M_3 and of the condyle, and appreciably above the upper margin of the fossa for the insertion of the *pars reflexa* (Fig. 1D–E).

The deep fossa lateral to the inflected angle (Fig. 1B, D; PIE) is clearly the fossa of insertion of the

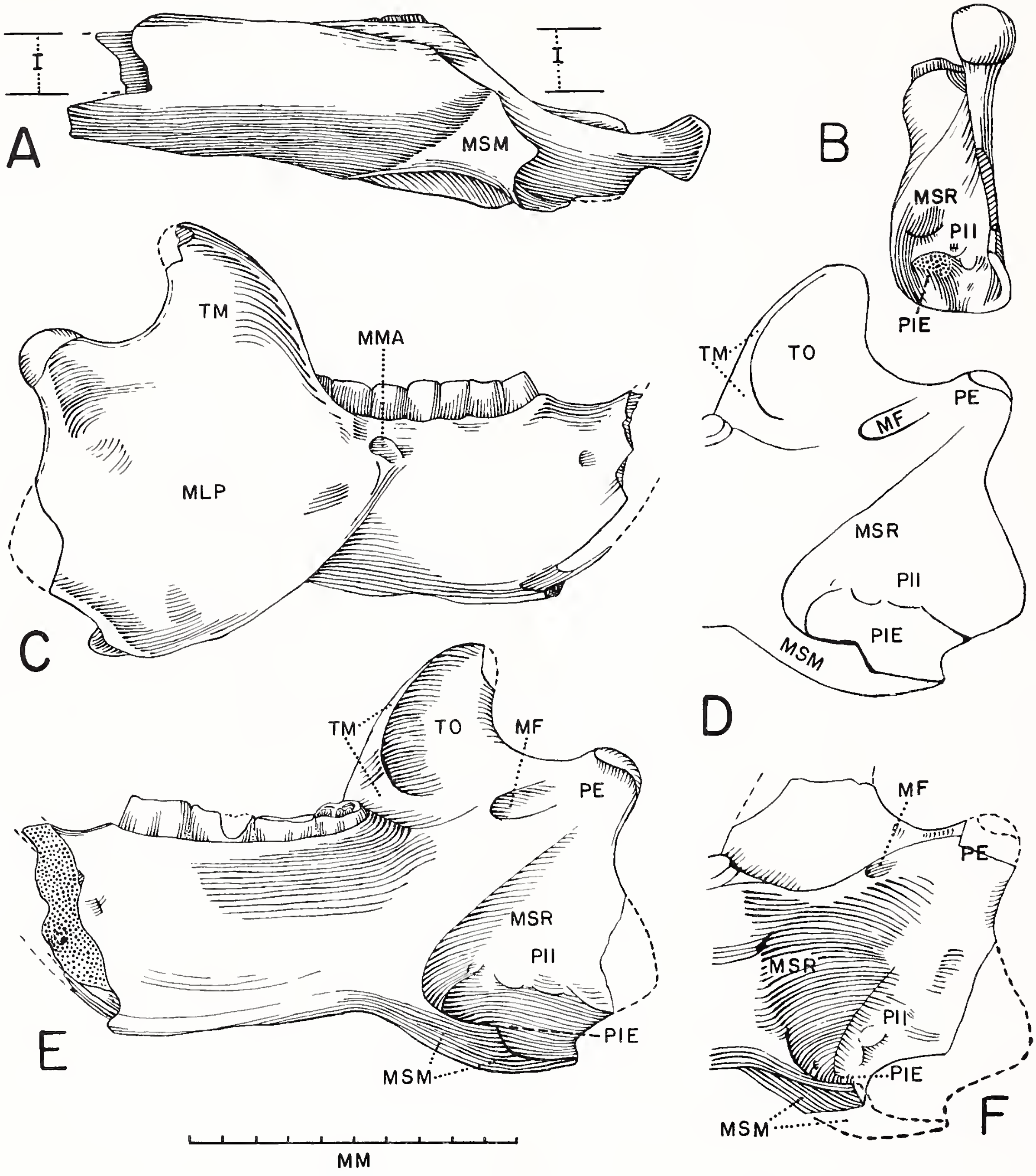

Fig. 1.—Right lower jaws of *Cylindrodon fontis,* ×5 (Scale bar, in mm, applies to all figures): A–E, A.M.N.H. no. 94501. A. Ventral view, B. Posterior view. C. Lateral view showing horizontal ramus disappearing behind angular process. D. Posterior part of medial view, showing muscle insertions. E. Medial view. F, A.M.N.H. no. F:AM 105370, medial view of posterior part.

Abbreviations: I-I, plane of lower incisor. MF, mandibular foramen. MLP, insertion of *Masseter lateralis profundus.* MMA, attachment of tendon of *Masseter medialis anterior.* MSM, insertion of main portion of *Masseter superficialis.* MSR, insertion of *Masseter superficialis, pars reflexa.* PE, insertion of *Pterygoideus externus.* PIE, insertion of *Pterygoideus internus,* external part. PII, insertion of *Pterygoideus internus,* internal part. TM, insertion of main part of *Temporalis.* TO, insertion of orbital part of *Temporalis.*

external portion of the *Pterygoideus internus* (Woods, 1972:131), which would seem to have been significantly larger in *Cylindrodon* than was the internal portion, whose area of insertion was slightly higher on the angle (Fig. 1D; PII). There do not seem to be any markings to indicate the limits of the insertion area of the *Pterygoideus externus* (Fig. 1D–E; PE).

A clearly marked crest along the median side of the anterior part of the coronoid process (Fig. 1D–E) forms the sharp boundary between the areas of insertion of the main part of the *Temporalis*, on the tip and anterior surface of the coronoid, and the orbital portion, inserting in the large fossa filling most of the median face of the coronoid (Woods, 1972:130).

The distribution of the various parts of the musculature in this area is thus similar in A.M.N.H. no. 94501 to what is found in modern caviomorphs (Woods, 1972:123–131).

However, rather surprising differences were noted on another jaw of *Cylindrodon fontis* in the American Museum collections, from Pipestone Springs, Montana (A.M.N.H. no. F:A.M. 105370), which likewise preserves a considerable portion of the mandible behind the cheek teeth (Fig. 1F). The hystricognathy and inflection of the angle is as pronounced as in the first specimen. There is no trace of either the pit within the fossa of the *Masseter superficialis, pars reflexa* or the deep pit for the external portion of the *Pterygoideus internus*. Instead, there is a pronounced groove separating the insertion of the *pars reflexa* not only from the external (as in A.M.N.H. no. 94501, Fig. 1D–E), but also from the internal, portion of the *Pterygoideus internus* (Fig. 1F). The insertion of the *pars reflexa* seems to have extended considerably higher on the mandible than in A.M.N.H. no. 94501, reaching nearly to the mandibular foramen (Fig. 1F), which is smaller than in A.M.N.H. no. 94501. Furthermore, in the posterior portion of the mandible that is preserved (Fig. 1F), there does not seem to be any visible separation between the insertions of the main and orbital portions of the *Temporalis*.

The musculature of the Mongolian cylindrodont *Ardynomys olseni* seems to show some differences from both of these specimens of *Cylindrodon*. In *Ardynomys*, the insertion of the *pars reflexa* apparently extended over the entire length of the posterior part of the jaw, being clearly visible below the condyle (Wood, 1970:Fig. 2a). As preserved, this specimen does not show the sharp demarcation between the fossa for the *pars reflexa* and that for the *Pterygoideus internus* seen in *Cylindrodon*. The lower jaw of the tsaganomyid *Cyclomylus lohensis* (Shevyreva, 1976:Fig. 12e, j) appears to have had muscular insertions very like those of *Ardynomys olseni*.

The significance of the apparent muscular variants among cylindrodonts is difficult to determine. The portions of the specimens present are very well preserved, and there is no indication of differential post-mortem abrasion. It seems most probable that there was considerable variation among cylindrodonts in the jaw musculature, perhaps indicating that active evolution of these features was in progress. It is possible that A.M.N.H. no. 94501 came from considerably later in the Chadronian than Pipestone Springs (see Wood, 1980*a*:59, correlation table, for relative ages within the Chadronian). If this is the case, it could indicate a reduction in the size of the *Masseter superficialis, pars reflexa*, and a considerably augmented differentiation between the two parts of the *Pterygoideus internus* and of the *Temporalis* during this interval. These differences between *Ardynomys olseni* and *Cylindrodon fontis* could merely be allometric (since the former is about twice the size of the latter), or they might indicate evolutionary divergence. Certainly they seem to indicate that *Ardynomys* was more closely related to the Tsaganomyidae than was *Cylindrodon*.

DISCUSSION

If the postulate stated above, that incipient hystricognathy originated only once among the Rodentia, is correct, the presence of hystricognathy in the early Oligocene *Cylindrodon* would mean that such a mid-Eocene ancestral cylindrodont as *Mysops* (Wilson, 1949*a*:94) must have been at least incipiently hystricognathous, presumably about as much so as was its contemporary, *Reithroparamys* (Wood, 1962:Fig. 41e), or the latest Paleocene (Wood, 1974*a*: 16–17) *Franimys* (Wood, 1962:Fig. 48d). There clearly was a distinct Middle American (as that term is defined by Ferrusquía, 1978:198) rodent fauna (Wood, 1974*a*:102–104), which included at least one middle Eocene species of *Mysops* (Wood, 1973:13–21) as well as the early Oligocene cylindrodont Subfamily Jaywilsonomyinae (Wood, 1974*a*:53).

Although it is obvious that we know only a small part of this Middle American fauna, what we do know is enough to indicate that the fauna as a whole must have been quite diverse, beginning at least as early as the middle Eocene (Wood, 1973).

The origins of the South American Caviomorpha have been the subject of extensive argument, some authors proposing an African origin and others an origin from Middle America (summarized by Lavocat, 1976:69–86, and by Patterson and Wood, 1982: 449–522, respectively). One of the factors that has prevented any agreement as to the ancestry of the caviomorphs is that there have been no hystricognathous rodents known from any part of the world that could have been truly ancestral to the caviomorphs. Lavocat (1976:69–86) has argued that unknown Eocene ancestors of the early Oligocene thryonomyoids of Egypt were such ancestors; Wood (1973:30–33; 1974*b*:31–33; 1975:78; 1977*b*:104–105; 1981:83–88; 1983:390) and Patterson and Wood (1982:458–459) have nominated unknown relatives of some of the known middle to late Eocene North and Middle American hystricognaths. But, in either case, the postulated ancestors were unknown animals with hypothetical morphology.

Lavocat (1973:163) reported an isolated tooth of what he thought to be a thryonomyoid ancestor from the Eocene of Pakistan: Hussain et al. (1978) described, as the Family Chapattimyidae, a number of Pakistani Eocene forms that they thought were such ancestors (as well as being ancestral to the contemporaneous North American Cylindrodontidae), but all of the known jaws that they refer to the Chapattimyidae are sciurognathous; the cheek-tooth pattern of "chapattimyids" is more suggestive of the Ctenodactylidae than of the Thryonomyoidea; and there is no indication, in any of the genera that Hussain et al. refer to the Chapattimyidae, of the delayed replacement of the deciduous teeth that is an outstanding characteristic of all known members of the Thryonomyoidea.

The much greater diversity of the early Oligocene caviomorphs than of the contemporary thryonomyoids in Africa strongly suggests that rodents had been in South America considerably longer, before the beginning of the Oligocene, than they had been in Africa, and makes it quite likely that they had arrived in South America very shortly after Musters (middle Eocene) time (Patterson and Wood, 1982: 471; Wood, 1983). We therefore should look among middle Eocene rodents for possible caviomorph ancestors.

The discovery that *Cylindrodon* (and presumably the remainder of the family as well) was hystricognathous greatly increases the significance of the dental similarities of the early Oligocene Jaywilsonomyinae to the Deseadan caviomorphs, previously commented on by Wood (1974*a*:53). There are no known dental features that would prohibit the cylindrodont *Mysops boskeyi,* from the middle Eocene of southern Texas (Wood, 1973:Figs. 3–4) from having been close to, if not actually, the ancestor of the brachydont Deseadan caviomorphs *Platypittamys, Migraveramus, Deseadomys,* and *Xylechimys.* The only other brachydont Deseadan rodent, *Protosteiromys,* had slightly more complex upper molars (Wood and Patterson, 1959:Fig. 30). It could be a slightly more evolved derivative from the same ancestral type, or it might represent the descedant of a second Middle American invader of South America, of a type still not recognized in Middle America, assuming that the Erethizontidae are as distinct from the other caviomorphs as has sometimes been proposed (Vanzolini and Guimarães, 1955*a*:30; 1955*b*:346; Moody and Doninger, 1956: 52–53; Bugge, 1974:56, 70, 71, 73).

We now at last have actual fossils of animals that lived in a possible source area for caviomorph ancestors, at what seems a suitable time to have allowed for the development of the known amount of early Oligocene (Deseadan) caviomorph diversity, and that had a tooth pattern less complex than, but potentially ancestral to, that of the most primitive of the Deseadan caviomorphs. I confidently expect that further work in the Eocene of Middle America will produce further evidence of caviomorph affinities among the rodents of this area. Furthermore, it should be emphasized that these Middle and North American Eocene franimorphs are the only Eocene rodents known from any part of the world that combine incipient hystricognathy with a tooth pattern that could have led to that of the Caviomorpha.

LITERATURE CITED

BLACK, C. C. 1963. A review of the North American Tertiary Sciuridae. Mus. Comp. Zool., Harvard Univ., Bull. 130:109–248.

———. 1965. Fossil mammals from Montana. Part 2. Rodents from the early Oligocene Pipestone Springs Local Fauna. Ann. Carnegie Mus., 38:1–48.

Black, C. C., and J. J. Stephens III. 1973. Rodents from the Paleogene at Guanajuato, Mexico. Occ. Papers Texas Tech Univ. Mus., 14:1–10.

Brandt, J. F. 1855. Beiträge zur nähern Kenntniss der Säugethiere Russlands. Mém. Acad. Imp. St. -Pétersbourg (6), 9:1–375.

Bugge, J. 1974. The cephalic arterial system in Insectivores, Primates, Rodents and Lagomorphs, with special reference to the systematic classification. Acta Anat., 87 (Suppl. 62): 1–160.

Burke, J. J. 1935. Pseudocylindrodon, a new rodent genus from the Pipestone Springs Oligocene of Montana. Ann. Carnegie Mus., 25:1–4.

Ellerman, J. R. 1940. The families and genera of living rodents. Vol. I. Rodentia other than Muridae. Brit. Mus. (Nat. Hist.), London: xxvi + 1–689.

———. 1941. The families and genera of living rodents. Vol. 2. Muridae. Brit. Mus. (Nat. Hist.), London: xii + 1–690.

Engesser, B. 1979. Relationships of some insectivores and rodents from the Miocene of North America and Europe. Bull. Carnegie Mus. Nat. Hist., 14:1–68.

Fahlbusch, V. 1970. Populationsverschiebungen bei tertiären Nagetieren, eine studie an oligozänen und miozänen Eomyidae Europas. Bayer. Akad. Wiss., Math.-Naturwiss. Kl., Abh., n.f., 145:1–136.

Ferrusquía-Villafranca, I. 1978. Distribution of Cenozoic vertebrate faunas in Middle America and problems of migration between North and South America. Chap. 13 of Conexiones terrestres entre Norte y Sudamerica (I. Ferrusquía-Villafranca, ed.). Bol. Univ. Nal. Auton. Mexico, Inst. Geol., 101:193–321.

Hoffstetter, R. 1973. Origine, compréhension et signification des taxons de rang supérieur: quelques enseignments tirés de l'histoire des mammifères. Ann. Paléont. (Vertébrés), 59: 137–169.

Hussain, S. T., H. DeBruijn, and J. H. Leiders. 1978. Middle Eocene Rodents from the Kala Chitta Range (Punjab, Pakistan). Proc. Konink. Nederlandse Akad. Wetenschappen (B), 81:74–112.

Korvenkontio, V. A. 1934. Mikroskopische Untersuchungen an Nagerincisiven unter Hinweis auf die Schmeltzstruktur der Backenzähne. Histologisch-phyletische Studie. Ann. Zool., Soc. Zool.-Bot. Fennicae Vanamo, 2:xiv + 1–274.

Landry, S. O. 1957. The interrelationships of the new and old world hystricomorph rodents. Univ. California Publ. Zool., 56:1–118.

Lavocat, R. 1951. Le parallélisme chez les rongeurs et la classification des porcs-épics. Mammalia, 15:32–38.

———. 1954. Sur l'importance des phénoménes de parallélisme dans l'évolution. C. R. 19th Internat. Geol. Congr., 1952, pt. 19:125–129.

———. 1955. Sur les relations systématiques entre les Théridomyidés et divers Rongeurs fossiles d'Afrique. C. R. Acad. Sci. Paris, 240:634–635.

———. 1973. Les rongeurs du Mioeène d'Afrique Orientale. 1. Miocène inférieur. Ecole Pratique des Hautes Etudes, Institut de Montpellier, Mém. 1:iv + 1–284. Separate folder of plates.

———. 1976. Rongeurs caviomorphes de l'Oligocène de Bolivie. II. Rongeurs du Bassin Déséadien de Salla-Luribay. Palaeovertebrata, 7:15–90.

Matthew, W. D., and W. Granger. 1925. New creodonts and Rodents from the Ardyn Obo Formation of Mongolia. Amer. Mus. Novit., 193:1–7.

Miller, G. S., and J. W. Gidley. 1918. Synopsis of the supergeneric groups of rodents. J. Washington Acad. Sci., 8: 431–448.

Moody, P. A., and D. A. Doninger. 1956. Serological light on porcupine relationships. Evolution, 10:47–55.

Patterson, B., and A. E. Wood. 1982. Rodents from the Deseadan Oligocene of Bolivia and the relationships of the Caviomorpha. Mus. Comp. Zool. Harvard Univ., Bull. 149: 371–543.

Schaub, S. 1953. Remarks on the distribution and classification of the "Hystricomorpha". Verh. Naturf. Ges. Basel, 64:204–210.

———. 1958. Simplicidentata (=Rodentia). Pp. 649–818, *in:* Traité de paléontologie, 6(2). (J. Pivetaeu, ed.). Masson, Paris.

Shevyreva, N. S. 1976. Paleogenovie Grizhuni Azhii (Semeistva Paramyidae, Sciuravidae, Ischyromyidae, Cylindrodontidae) [Paleogene rodents of Asia (Families Paramyidae, Sciuravidae, Ischyromyidae, Cylindrodontidae)]. Akad. Nauk SSSR, Trudi Paleontol. Inst., 158:1–116.

Simpson, G. G. 1945. The principles of classification and a classification of Mammals. Bull. Amer. Mus. Nat. Hist., 85: xvi + 1–350.

Thaler, L. 1966. Les rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe. Mus. Nat. Hist. Nat., Mém., new ser. (C), 17:1–295.

Tullberg, T. 1899. Ueber das System der Nagethiere: eine phylogenetische Studie. Nova Acta Reg. Soc. Scient. Upsala (3) 18:i–v, 1–514.

Vanzolini, P. E., and L. R. Guimarães. 1955*a*. Lice and the history of South American land mammals. Rev. Brasiliera Entomolog., 3:13–46.

———. 1955*b*. South American land mammals and their lice. Evolution, 9:345–347.

Vianey-Liaud, M. 1972. L'évolution du genre *Theridomys* à l'Oligocène moyen. Intérêt biostratigraphique. Bull. Mus. Nat. Hist. Nat. (3), 98:295–371.

Wahlert, J. H. 1968. Variability in rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and recent rodent groups. Breviora, 309:1–18.

———. 1973. *Protoptychus,* a hystricomorphous rodent from the late Eocene of North America. Breviora, 419:1–14.

Waterhouse, G. E. 1839. Observations on the Rodentia, with a view to point out the groups, as indicated by the structure of the crania, in this order of mammals. Mag. Nat. Hist., new ser., 3:90–96.

Wilson, R. W. 1949*a*. Early Tertiary rodents of North America. Carnegie Inst. Washington, Publ. 584:67–164.

———. 1949*b*. On some White River fossil rodents. Carnegie Inst. Washington, Publ. 584:27–50.

Wood, A. E. 1935. Evolution and relationships of the Heteromyid Rodents, with new forms from the Tertiary of western North America. Ann. Carnegie Mus., 24:73–262.

———. 1936. Parallel radiation among the Geomyoid rodents. J. Mamm., 18:171–176.

———. 1937. Rodentia. Part 2 of The Mammalian Fauna of the White River Oligocene by W. B. Scott, G. L. Jepsen and A. E. Wood. Trans. Amer. Phil. Soc., new ser., 28:155–269.

———. 1947. Rodents—a study in evolution. Evolution, 1: 154–162.

———. 1950. Porcupines, paleogeography and parallelism. Evolution, 4:87–98.

———. 1955. A revised classification of the rodents. J. Mamm., 36:165–187.

———. 1959*a*. Are there Rodent suborders? Syst. Zool., 7:169–173 (dated Dec. 1958, but published in Jan. 1959).

———. 1959*b*. Eocene radiation and phylogeny of the rodents. Evolution, 13:354–361.

———. 1962. The early Tertiary Rodents of the Family Paramyidae. Trans. Amer. Phil. Soc., new ser., 52:1–261.

———. 1965. Grades and Clades among Rodents. Evolution, 19:115–130.

———. 1968. The African Oligocene Rodentia. Part 2. Early Cenozoic Mammalian Faunas, Fayum Province, Egypt. Bull. Peabody Mus. Nat. Hist., Yale Univ., 28:23–105.

———. 1970. The early Oligocene Rodent *Ardynomys* (Family Cylindrodontidae) from Mongolia and Montana. Amer. Mus. Novit., 2418:1–18.

———. 1972. An Eocene hystricognathous rodent from Texas: its significance in interpretations of continental drift. Science, 175:1250–1251.

———. 1973. Eocene rodents, Pruett Formation, southwest Texas; their pertinence to the origin of the South American Caviomorpha. Pearce-Sellards Series, Texas Mem. Mus., 20: 1–40.

———. 1974*a*. Early Tertiary vertebrate faunas, Vieja Group, Trans-Pecos Texas: Rodentia. Bull. Texas Mem. Mus., 21: 1–112.

———. 1974*b*. The evolution of the Old World and New World Hystricomorphs. Zool. Soc. London, Symp., 34:21–54; discussion, 55–60.

———. 1974*c*. Rodentia. Encyclopaedia Brittanica, 15th Ed., Macropaedia, 15:969–980.

———. 1975. The problem of the hystricognathous rodents. *In*: Studies on Cenozoic Paleontology and Stratigraphy in Honor of Claude W. Hibbard, Univ. Michigan Papers on Paleont., 12:75–80.

———. 1976. The Oligocene rodents *Ischyromys* and *Titanotheriomys* and the content of the Family Ischyromyidae. Pp. 244–277, *in* Athlon: Essays in palaeontology in honour of Loris Shano Russell (C. S. Churcher, ed.). Misc. Publ. Royal Ontario Mus. Life Sci.:1–286.

———. 1977*a*. The evolution of the rodent Family Ctenodactylidae. J. Palaeont. Soc. India, 20:120–137.

———. 1977*b*. The Rodentia as clues to Cenozoic migrations between the Americas and Europe and Africa. Pp. 95–109, *in* Paleontology and plate tectonics (R. M. West, ed.). Milwaukee Public Mus., Spec. Publ. Biol. & Geol., 2:v + 1–109.

———. 1980*a*. The Oligoeene rodents of North America. Trans. Amer. Phil. Soc. 70 (pt. 5):1–68.

———. 1980*b*. Problems of classification as applied to the Rodentia. Pp. 263–272, *in* Palaeovertebrata, Mém. Jubil. R. Lavocat (J. Michaux, ed.):1–382.

———. 1981. The origin of the caviomorph rodents from a source in Middle America: a clue to the area of origin of the Platyrrhine Primates. Pp. 79–91, *in* Evolutionary biology of the New World monkeys and continental drift (R. L. Ciochon and A. B. Chiarelli, eds.), Plenum Publ. Corp., New York:xvi + 1–528 (dated 1980, but not published until March 1981).

———. 1983. The radiation of the Order Rodentia in the southern continents; the dates; numbers and sources of the invasions. Schriftenr. Geol. Wiss. (1983), 19/20:381–394.

WOOD, A. E., AND B. PATTERSON. 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution. Mus. Comp. Zool., Harvard Univ., Bull. 120:279–428.

———. 1970. Relationships among hystricognathous and hystricomorphous rodents. Mammalia, 34:628–639.

WOODS, C. A. 1972. Comparative myology of jaw, hyoid and pectoral appendicular regions of New and Old World hystricomorph rodents. Bull. Amer. Mus. Nat. Hist., 147:117–198.

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SKELETONS OF THE DIMINUTIVE SABERTOOTH *EUSMILUS* FROM THE ARIKAREEAN OF SOUTH DAKOTA

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ABSTRACT

Associated partial skeletons of a juvenile and an adult diminutive sabertoothed carnivore from Washabaugh County, South Dakota, include the first known postcranial material of *Eusmilus* Gervais, 1876. *Hoplophoneus belli* Stock, 1933 and *Ekgmoiteptecela olsontau* Macdonald, 1963 are found to be synonyms of *Hoplophoneus cerebralis* Cope, 1880. That species is referable to *Eusmilus* and should be known as *Eusmilus cerebralis* (Cope). Adult individuals of *E. cerebralis* were probably about the size of the living bobcat *Felis* (*Lynx*) *rufa*, although their skeletons are more robust and muscle scars indicate that these animals, while small, were powerfully built.

INTRODUCTION

In the summer of 1978 I collected two partial skeletons of small sabertoothed carnivores in Washabaugh County, South Dakota. The remains were so closely associated, and so fragmentary and disarticulated, that the presence of more than one individual did not become apparent until nearly all the fragments had been washed and sorted. Whether the animals died of disease or injury, and whether they were mother and offspring or unrelated, is left to speculation.

Remains of diminutive sabertooths are extremely rare in the North American Tertiary; only four published specimens, and perhaps an equal number of unpublished specimens, are known. The relative completeness of the two skeletons described in this paper, including skulls, jaws, and postcranial elements, not only makes possible direct comparison of the three described species of small sabertooths, *Hoplophoneus cerebralis, H. belli,* and *Ekgmoiteptecela olsontau,* but also reveals a wealth of detail about their ontogeny and postcranial morphology, formerly undescribed.

Acronyms.—AMNH, American Museum of Natural History, New York, New York; LACM, Los Angeles County Museum of Natural History, Los Angeles, California; PU, Geological Museum, Princeton University, Princeton, New Jersey; SDSM, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota; UCMP, University of California Museum of Paleontology, Berkeley, California.

Locality.—UCMP V79034, Two Cat. This locality is in the White River Badlands, south of the White River and east of Bear-in-the-Lodge Creek, Washabaugh County, South Dakota. Detailed locality information is on file in the Museum of Paleontology, University of California, Berkeley, California.

Stratigraphy and chronostratigraphic age.—In most of the White River Badlands the typically pinkish-tan overbank deposits of the Brule Formation (Orellan-Whitneyan) are conformably overlain by the Rockyford Ash Member or the pale tan massive siltstones of the upper member of the Sharps Formation (Arikareean). Near UCMP V79034 this apparently is not the case. Some 100 meters of channel deposits of various lithologies lie between what seems to be the typical Brule and Sharps Formations. These intervening deposits probably represent a facies of the Sharps Formation not seen in its type area some 40 km west of UCMP V79034, in Shannon County, South Dakota. The beaver *Palaeocastor* occurs throughout the channel deposits stratigraphically above and below UCMP V79034; it is typical of Arikareean faunas. It is likely that the southeastern White River Badlands would produce an Arikareean fauna reflecting environmental or depositional conditions quite different from those of the Sharps Formation fauna as described by Macdonald (1963, 1970), collected only 40 km to the west.

J. C. Harksen (field notes, 1977) assigned letter designations from A through U to units of the channel deposits in the vicinity of UCMP V79034, beginning at the top with typical Sharps Formation and proceeding downward. Unit U appears to be the top of the Scenic Member of the Brule Formation. Harksen designated the horizon of UCMP V79034 as L and described its lithology as wormy tan silty ash with some vertical joint faces. Unit L is some 2 m thick.

MATERIALS

The two specimens of *Eusmilus cerebralis* described in this paper are UCMP 123180, an adult partial skeleton, and UCMP 123181, a juvenile partial skeleton. Most of the elements preserved in both specimens are fragmentary. What remains, however, is generally well preserved.

Faint cartilaginous lines between epiphyses and shafts of the limb bones indicate that the adult individual (UCMP 123180) was not fully mature. Some of the vertebral epiphyses, especially those on the thoracic vertebrae, are not completely fused. The juvenile specimen (UCMP 123181) retains epiphyses only on the proximal end of the right humerus and the anterior end of the right ilium. Table 1 lists the elements present in each specimen; measurements of selected elements are given in Table 2.

TAXONOMY

Hatcher (1895) referred the first North American sabertoothed carnivore specimen (PU 11079) to *Eusmilus*. He, and subsequent workers, thought that the long, laterally compressed upper canine, the extremely deep dentary flange, and the reduction of the cheek tooth number established generic identity of the large North American specimens with the smaller specimens of *Eusmilus* known from Europe.

Macdonald (1963:221) diagnosed *Ekgmoiteptecela*, from the Sharps Formation (Arikareean) of Shannon County, South Dakota, as a "small, short-faced cat with dentition like that of *Eusmilus* Gervais, 1875." (It should be noted that although 1875 is frequently given as the date of publication for *Eusmilus* the actual date was 1876. The correct citation is given in the literature cited at the end of this paper.) The type specimen of *Ekgmoiteptecela olsontau* (SDSM 54247) apparently represents a short-faced individual, and that, coupled with its small size, distinguished it from the large, long-faced *Eusmilus sicarius* and *Eusmilus dakotensis* (Orellan and Whitneyan) found in the Brule Formation in

Table 1.—*Elements preserved.*

UCMP 123180 (adult)	UCMP 123181 (juvenile)
Skull: Partial maxillae, jugals, frontals, squamosals, parietals, temporals, petrosals, basisphenoid, occipital	Nasal, frontals, maxillae, parietals, jugals, squamosal, temporal, petrosals, occipital
Dentary: Fragments of horizontal rami, flanges	Horizontal rami, left condyle, left half of symphysis
Vertebrae: Atlas fragment, cervicals 4–7, thoracics 1–4, 7–9, 11, lumbars 2, 4, 6–7 (fragmentary)	Cervicals 1–7, thoracics 1, 2, 5–9, 11–13, lumbar 2 (fragmentary)
Sacrum: Present	Absent
Scapula: Right and left proximal ends	Right and left proximal ends
Humerus: Proximal ends, right distal end, left distal fragment	Proximal ends, right distal fragment
Ulna: Left proximal end	Left proximal end
Raduis: Right and left proximal and distal ends, shaft fragments	
Innominate: Right and left ilium and ischium fragments	Right and left anterior ilium and ischium fragments
Femur: Right and left proximal ends, left distal end	Right proximal end
Tibia: Right proximal end, shaft fragment, and distal fragment; left shaft, distal end	
Calcaneum: Left, nearly complete	
Astragalus: Left, nearly complete	
Sternebrae: Manubrium; mesosternum fragment	

Table 2.—*Measurements (in millimeters) of* Eusmilus cerebralis.

Measurements	UCMP 123180 (adult) a-p	UCMP 123180 (adult) trans	UCMP 123181 (juvenile) a-p	UCMP 123181 (juvenile) trans
Estimated snout–vent length	610.0		510.0	
Skull, approx. a-p dia.	110.0		95.0	
Rt. dentary, depth below P_4	18.0		—	
Rt. dentary, depth below dP_4	—		13.5	
Rt. P_4–M_1, a-p dia. (alveolar)	19.0		—	
Left P_4–M_1, a-p dia. (alveolar)	20.0		—	
Rt. M_1	—	—	13.3	—
Left dC_1 root	—	—	3.15	1.1
Left I_3 root	—	—	2.25	1.15
Left I_2 root	—	—	3.15	2.25
Left I_1 root	—	—	2.25	1.2
Rt. dP^3	—	—	ca. 10.0	2.9
Rt. dP^4	—	—	3.65	4.7
Rt. M^1	—	—	4.0	4.2
Atlas	—	—	18.4	36.0
Axis	—	—	24.0	20.0
4th cervical, centrum	12.8	—	9.2	—
1st thoracic, centrum	11.7	—	7.9	—
11th thoracic, centrum	13.5	—	11.0	—
13th thoracic, centrum	—	—	9.5	—
2nd lumbar, centrum	19.0	—	12.7	—
4th lumbar, centrum	19.9	—	—	—
7th lumbar, centrum	17.5	—	—	—
Sacrum	45.2	32.0	—	—
Rt. scapula, glenoid fossa	16.8	11.25	—	—
Left scapula, glenoid fossa	—	—	11.3	8.75
Rt. humerus, prox. end	—	—	19.0	13.0
Left humerus, prox. end	24.2	24.2	—	—
Rt. humerus, dist. end	13.6	28.5	—	—
Left humerus, dist. end	—	—	8.85	—
Left radius, prox. end	8.8	12.0	—	—
Left radius, dist. end	11.5	16.85	—	—
Rt. femur, prox. end	—	—	10.5	18.6
Left femur, prox. end	13.7	30.5	—	—
Left femur, dist. end	20.0	24.0	—	—
Rt. tibia, prox. end	24.0	22.3	—	—
Left tibia, dist. end	12.6	16.6	—	—
Femur, estimated length	119.0		—	—
Tibia, estimated length	112.0		—	—
Left calcaneum, length	31.0		—	—
Left astragalus, max. width	9.5		—	—
Femorotibial index*	94.1		—	—

* Tibia length/femur length × 100.

the White River Badlands only a few kilometers from, and a short distance stratigraphically below, the type locality of *Ekgmoiteptecela olsontau.*

A number of students of fossil carnivores now believe that the large North American Oligocene species formerly known as *Eusmilus* should be referred to *Hoplophoneus,* and that the diminutive sabertooths—*Hoplophoneus cerebralis* Cope, 1880, *H. belli* Stock, 1933, and *Ekgmoiteptecela olsontau* Macdonald, 1963—represent the only actual occurrences of *Eusmilus* in North America (Toohey, 1959; Morea, personal communication; Martin, 1980). These three taxa, and a few undescribed specimens, have been found in rocks of late Oligocene/early Miocene age in the Great Plains, eastern Oregon, and southern California. Morea (personal communication) believes that *H. belli* is a synonym of *H. cerebralis,* and that *H. cerebralis* should be referred to *Eusmilus.* Morea (personal communication) further believes that *Ekgmoiteptecela olsontau* probably would be found to be a synonym of *Eusmilus cerebralis* (Cope) if skulls and dentaries of the former were found in association. The associated skulls and dentaries described in this paper make possible the direct comparison of all three taxa.

The skull of the adult animal (UCMP 123180), although fragmentary and edentulous, closely resembles Cope's type of *Hoplophoneus cerebralis* (AMNH 6941) and the type of *H. belli* (LACM 463) in general outline, shape of the canine alveolus, dental formula, large postorbital processes, high, vertical occiput, and long mastoid processes and glenoid pedicles. The associated lower jaws of UCMP 123180, likewise fragmentary and edentulous, compare well with SDSM 54247, the type dentary of *Ekgmoiteptecela olsontau,* in dental formula, inferred relative size and position of the cheek teeth, position of the coronoid fossa, and position and size of the flange. For these reasons I think both *Hoplophoneus belli* and *Ekgmoiteptecela olsontau* should be considered junior synonyms of *Hoplophoneus* [=*Eusmilus*] *cerebralis* Cope. Morea's decision (personal communication) to use the new combination *Eusmilus cerebralis* (Cope) appears to me to be entirely justified.

OSTEOLOGY

Skull.—In the adult, UCMP 123180, the occipital region of the skull rises vertically to a high, rounded lambdoidal crest (Fig. 1). The sagittal crest is thin, low, and short. A thin median supraoccipital ridge extends from the foramen magnum to the lambdoidal crest. As in *Hoplophoneus,* the mastoid processes and glenoid pedicles are greatly elongated. Beneath the thin parietals is an endocranial cast in the cerebral fossa. The postorbital processes appear to have been large. Portions of a large infraorbital foramen and a small lacrimal canal remain. The upper canines are broken away, but what remains of their alveoli suggest that they were extremely compressed laterally and that their roots reached a point just above the anterior border of the orbits. Posterior to the alveolus of the left canine are the two small roots of P^3.

Fracturing of the skull by natural means has exposed the endocranial cast, the frontal sinuses, and the internal auditory regions. The endocast closely resembles one identified as *Eusmilus* (Radinsky, 1971:fig. 3A). Radinsky's terminology for features of the endocast (1969, 1971) is used here. On the dorsal surface of the endocast the sagittal, lateral, and suprasylvian sulci are visible. The dorsal portion of the ectosylvian sulcus can be seen on the left side, and appears to be strongly arched. The supraorbital sulcus is deep and well defined. There is no evidence of a cruciate sulcus. The posterior portion of a rounded olfactory bulb is present on the left side. Although this is a rather simple brain, it shows the beginnings of cortical complicaton which would increase motor control and tactile sensitivity (Radinsky, 1971:521).

Two frontal sinuses lie on either side of the dorsal midline where they are exposed in cross section in the postorbital constriction. Nearest the midline is a narrow sinus, and dorsolateral to it a larger one which is just dorsal to the orbit. Bone over the area of the cerebrum is 2 to 3 mm thick. Anterior to the brain cavity the skull roof thickens to include the frontal sinuses, but laterally it remains thin.

Both tympanic bullae have been broken away in UCMP 123180. The petrosals are exposed to ventral, medial, and dorsal view, and the left petrosal is cracked, partly exposing the coils of the cochlea. A large foramen on the dorsal surface of the petrosal carried the cochlear branch of the auditory nerve (VIII). Part of the posterior horn of the left tympanic ring is exposed.

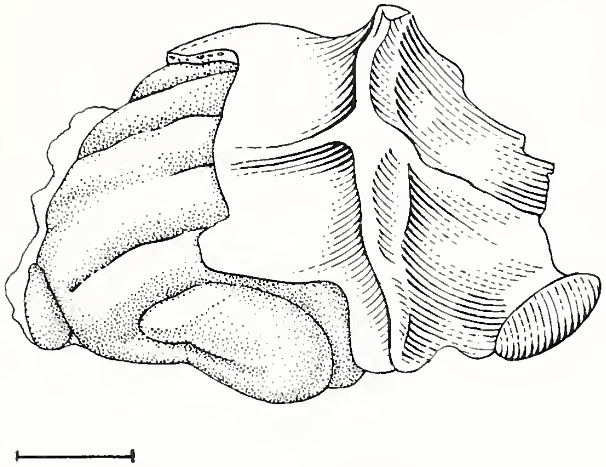

Fig. 1.—*Eusmilus cerebralis*, UCMP 123180. Posterior cranium fragment. Left dorsolateral view, endocast stippled. Left occipital condyle at lower right. Scale bar equals 1 cm.

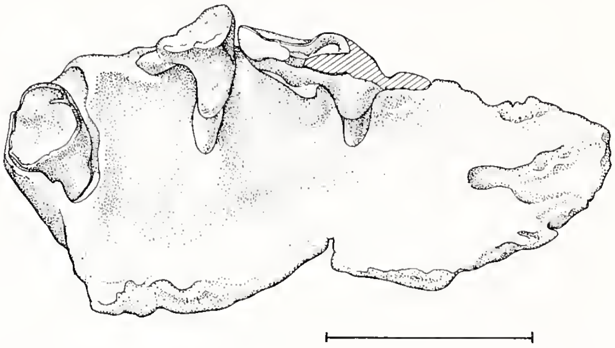

Fig. 2.—*Eusmilus cerebralis*, UCMP 123181. Right maxilla with dP^3–dP^4 and M^1. Occlusal view. Scale bar equals 1 cm.

Part of what seems to be the posterior lacerate foramen remains on a fragment of the basioccipital. Although this fragment does not contact any other, it appears that the posterior lacerate foramen lay near the posteromedial border of the tympanic bulla.

The incomplete nature of the juvenile skull (UCMP 123181) precludes an accurate determination of its dimensions; it was perhaps 20% smaller than that of the adult. Several of its features are probably age-related; for example, the lambdoidal crest is low, there is no sagittal crest, the mastoid processes and glenoid pedicles are short, and the horizontal rami of the dentaries are shallow. Large postorbital processes curve ventrolaterally away from the skull roof. The exposed ventral surface of the frontals shows the positions of sagittal, lateral, and supraorbital sulci on the brain, and the olfactory bulbs. The left petrosal bears a fragment of the anterior horn of the tympanic ring. Where the frontals are broken near their contact with the maxillae, roots of both permanent and deciduous canines are exposed in cross section, just anterior to the orbits. The deciduous canine root, oval in cross section and only 1.5 mm in transverse diameter, lies medial to the larger (2.2 mm transverse diameter) root of the permanent canine.

The right maxilla (Fig. 2) of the juvenile specimen contains dP^{3-4} and M^1. The broken dP^3 is blade-like and three-rooted. There is a large, vertical posterior root, a somewhat smaller, anteriorly-slanted anterior root, and a small anterolingual root which seems to have acted as a buttress for the blade rather than in support of a cusp. The dP^4 is roughly triangular, wider than long, and three-rooted. Crests extend from the three corners of the tooth to a central cusp, and there is a low labial cingulum. M^1 is a small rounded peg just erupting from the maxilla. Its nearly featureless crown slopes posterodorsally. The palate is deeply excavated between dP^3 and dP^4 and between dP^4 and M^1, forming a bony ridge extending lingually from dP^4. A fragment of the anterior part of the jugal adheres to the fragment of maxilla on the lower border of the orbit. A tiny fragment of the left maxilla, also with a small portion of the jugal attached, is broken to expose the posterior half of the unerupted P^4, a transversely flattened blade about 7 mm in height. There is a minute carnassial notch but no evidence of roots on this tooth.

Dentary.—Both dentaries of the adult are fragmentary; no teeth are preserved, and the ascending rami and most of the symphysis are absent. The posterior root of M_1 is small, the anterior root larger. Although the posterior root of P_4 is wider than the anterior, the two are essentially subequal in size. The coronoid fossa extends anteriorly to a point just posteroventral to the posterior root of M_1. The most extraordinary feature of the dentary is the deep flange which protected the upper canine. Although both flanges are preserved in UCMP 123180, they do not contact the fragments of the horizontal rami. Relationships between these fragments can be inferred from a juvenile right dentary, LACM 5465, which Macdonald (1970:68) referred to *Ekgoiteptecela olsontau*. Depth of the flanges apparently increased until maturity; those of the juvenile, LACM 5465, are smaller than those of UCMP 123180, a young adult. The flanges met in a deep median symphysis. Only some 7 mm at the ventral tips remained free.

Lateral surfaces of the flanges lay about 20 mm apart along the anterior margins. UCMP 123180 shows no evidence of the large mental foramen seen in the type specimen of *E. olsontau* (SDSM 54247), but the referred right dentary (LACM 5465) also lacks one. There are two small foramina on the anterior face of the right flange in UCMP 123180, one near the ventral tip and another about 12 mm dorsal to it. Flange shape, and position and shape of the foramina on the anterior dentary, are highly variable in sabertoothed carnivores (Baskin, 1981). A prominent knob on the medial surface of the dentary, posteroventral to the posterior root of M_1, was probably the point of attachment for the pterygoideus muscle, which adds power to the bite and restrains the jaws, preventing disarticulation.

The left dentary of the juvenile specimen (UCMP 123181) is fairly complete, lacking only the flange and posterior portion of the jaw. The right dentary is much less complete, and all erupted teeth in both dentaries are broken away.

The condyle is wide and nearly cylindrical, though it tapers to a blunt point medially. The broken anterior edge of the condyle fragment indicates that the angle was inflected. The coronoid fossa extends to a point ventral to the posterior root of dP_4. The horizontal ramus is shallow below the cheek teeth and in the region of the diastema posterior to the canine, a feature which is apparently age-related. The horizontal ramus is relatively deeper in the known adult specimens.

I prepared the right dentary fragment of UCMP 123181 to reveal the unerupted permanent dentition. M_1 consists of protoconid and paraconid only. Faint notches along the posterior border of the protoconid suggest the presence of metaconid and talonid but probably would be obliterated after only a little wear. A strong vertical ridge extends from the base to the apex of the protoconid on its lateral surface. The anterior border of the slightly shorter paraconid is convex anteriorly. Only the bluntly pointed apex of the posterior cusp of P_4 remains. Both the P_4 fragment and M_1 closely resemble their counterparts in the type of *Eusmilus bidentatus* Gervais and in PU 11079, which Hatcher (1895) described as the type of *E. dakotensis*, in morphology if not in size. Progressive reduction of the posterior cusps of M_1 appears to have been a trend common both to later North American hoplophonines and to *Eusmilus* (*sensu stricto*).

Roots of the deciduous teeth indicate the presence of dP_3 and dP_4. Proportions of the crowns cannot be inferred from UCMP 123181, but these teeth are present in the juvenile right dentary (LACM 5465) which Macdonald (1970) referred to *Ekgmoiteptecela olsontau*. Preservation of LACM 5465 is poor, but it does retain a small, very much worn dP_3 which overlaps labially the high and less worn blade of dP_4. The dP_4 is partly displaced upward by the eruption of M_1 from below and posterior to it. In most carnivores the permanent carnassial emerges almost directly posterior to the deciduous carnassial, but reduction of the cheek tooth dentition in *Eusmilus cerebralis* appears to have been accompanied by crowding of the remaining teeth, both deciduous and permanent.

Roots of the canines and incisors in UCMP 123181 are visible in a fragment of the dentary symphysis. The permanent canine can be seen in cross section where the dentary is broken, through the diastema region. A small, narrow root of the deciduous canine remains in the alveolus. Whether the incisor roots are those of the deciduous or permanent teeth is impossible to determine, so I will simply refer to them as I_1, I_2, and I_3 for convenience. The root of I_3 lies directly anteromedial to the deciduous canine root; it is small and circular in section. Medial to it is the root of I_2, largest of the incisors. Anteromedial to I_2 is the root of I_1, a fragile structure which lies in the symphysis and is the smallest of the anterior teeth.

Atlas.—The left side of the atlas, lacking most of the wing, is preserved in the adult specimen, UCMP 123180. The prezygapophysis is deeply concave; the postzygapophysis is quite flat and lies at about 50° to the sagittal plane. Remains of the wing suggest that it was thin anteriorly and thicker posteriorly where it contained the intervertebral canal. Whether the wing had a posterolateral spine as in *Smilodon* cannot be determined. In the juvenile (UCMP 123181) the atlas is complete. The wings are small, with rounded borders and no suggestion of a spine. In this specimen the ventral arch of the atlas is short anteroposteriorly (4.3 mm) and the dorsal arch is long (10.3 mm).

Axis.—Only the juvenile (UCMP 123181) axis is preserved. There is a short, thick spine, and the prezygapophyses lie at about 50° to the sagittal plane. The anterior face of the axis thus appears flatter in dorsal view than is usual in felines, in which the angle of the prezygapophyses is about 35° to the sagittal plane.

Cervical vertebrae.—In the adult (UCMP 123180) the known cervical vertebrae (4–7) each have a strong

Table 3.—*Measurements and proportions of the sacrum (in mm).*

Species and museum no.	(A) Trans. dia. of ant. centrum	(B) Trans. dia. of post. centrum	A/B
Felis (*Lynx*) *canadensis* (UCMP 58547)	17.6	8.3	2.12
Eusmilus cerebralis (UCMP 123180)	15.3	8.8	1.74
Felis concolor (UCMP 47164)	31.9	20.7	1.54

anteroposterior ridge along the ventral midline. The centra are not as steeply inclined anteriorly as in felines. In the juvenile (UCMP 123181), short neural spines on the third through the sixth cervical vertebrae fit into a notch on the neural arch of the preceding vertebra. The cervical series is preserved in tightly interlocked articulation.

Thoracic vertebrae.—Thoracic vertebrae of the adult (UCMP 123180) are represented only by the centra. The anterior thoracics seem disproportionately small for so robust an animal; the posterior thoracics are larger. The juvenile (UCMP 123181) thoracic vertebrae have wide, heavy transverse processes. The neural arches are low, and the neural spines on the posterior thoracics are very strongly swept back.

Lumbar vertebrae.—Lumbar vertebrae of the adult (UCMP 123180) are large and robust, and appear to have had strong transverse processes and neural spines. The only lumbar vertebra referable to the juvenile specimen (UCMP 123181), probably the second, is slightly longer than the last thoracic but much shorter proportionately than the same vertebra in the adult. A great deal of elongation in the lumbar region must have occurred during maturation in these animals.

In the adult specimen (UCMP 123180) the cervical and thoracic vertebrae have barely fused epiphyses; those on the lumbar vertebrae are much more strongly integrated. None of the vertebral epiphyses in the juvenile specimen (UCMP 123181) is fused with the centrum, and several rib fragments adhere to the thoracic vertebrae.

Sacrum.—The sacrum of the adult (UCMP 123180) consists of three fused vertebrae. Contact with the ilium was large and triangular. The sacrum narrows abruptly toward the tail and is downcurved posteriorly. Comparison of measurements of this element (Table 3) with those of the sacrum of *Felis concolor* (UCMP 47164), a long-tailed cat, and *Felis* (*Lynx*) *rufa* (UCMP 58547), a short-tailed cat, was not helpful in estimating tail length of *Eusmilus cerebralis.*

Sternum.—Two sternum fragments, the manubrium and a piece of the mesosternum, appear to belong to the adult animal (UCMP 123180). They seem robust for a cat of this size. The manubrium is keeled along its dorsal midline, rugose on the ventral surface, deep, and bluntly rounded anteriorly. The fragment of mesosternum is deeply grooved along its dorsal midline and roughly square in cross section.

Scapula.—Only the glenoid regions of the scapulae are preserved. In the adult (UCMP 123180) the glenoid fossa is kidney-shaped and moderately deep. The coracoid process, though broken, appears to have been large. The acromion is missing; the spine extends to within 10 mm of the border of the glenoid fossa.

In the juvenile (UCMP 123181) the glenoid fossae are shallower and narrower than in the adult. More of the spine is preserved in the juvenile specimen, suggesting that there was a prominent acromion which extended at least as far ventrally as the glenoid border.

Humerus.—Not enough of the humerus remains to allow any estimate of its total length in the adult animal (UCMP 123180). The proximal end has a large, round head separated from the pointed greater tuberosity by a narrow bicipital groove. A robust lesser tuberosity provided a large area of insertion for the M. subscapularis. Extending distally from the greater tuberosity is a strong deltoid crest, which, together with the large acromion, is indicative of a large and powerful deltoid muscle.

The distal end of the humerus (Fig. 3) is wide and anteroposteriorly flattened. A shallow, open groove separates the small capitulum from the steeply inclined trochlea. Low on the distal end is a very large entepicondylar foramen. The olecranon fossa is wide, shallow, and low.

In the juvenile specimen (UCMP 123181) the slender shaft of the humerus is extremely thin-walled. As in the adult specimen the distal end is much flattened anteroposteriorly and has a large entepicondylar foramen; the proximal end of the humerus resembles that of the adult, but comparison is difficult because of poor preservation of the epiphysis.

Ulna.—Only the proximal end of the left ulna (Fig. 4) is preserved in the adult specimen (UCMP 123180). The high olecranon process is narrow at its anterior border. A rectangular, rugose area con-

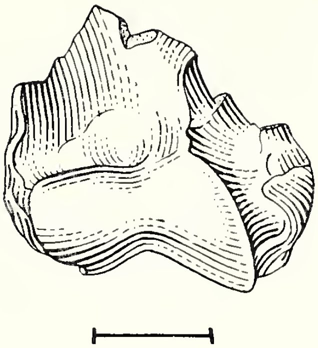

Fig. 3.—*Eusmilus cerebralis,* UCMP 123180. Right distal humerus, anterior view. Scale bar equals 1 cm.

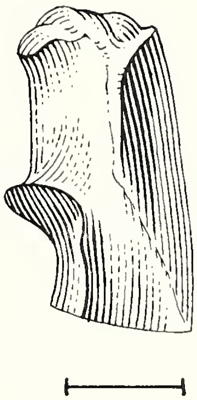

Fig. 4.—*Eusmilus cerebralis,* UCMP 123180. Left proximal ulna, lateral view. Scale bar equals 1 cm.

fined to the proximal surface of the olecranon indicates the area of insertion of the M. triceps brachii. A smooth, teardrop-shaped area covers the posterior face of the olecranon process. It probably was bounded by the insertion of the anconeus muscle laterally, and medially by the origin of the M. flexor carpi ulnaris. These large muscle scars are not developed on the proximal ulna fragment of the juvenile specimen (UCMP 123181), but more of the semilunar notch is preserved. It curves across the anterior face of the ulna, its proximal end protruding beyond the lateral surface of the bone, its distal lip extending beyond the medial side. A tiny radial facet is formed by a distal extension of the semilunar notch on the medial surface.

Radius.—The proximal articular surface of the radius in the adult animal (UCMP 123180) is a nearly featureless oval. The distal end has a strong styloid process, a diamond-shaped ulnar facet, and two shallow grooves for the tendons of the forefoot extensors on its cranial face, separated by a prominent dorsal tubercle. The distal articular surface is roughly diamond-shaped in outline. The articular surface for the scapholunar is not extensive and is rather flat. Total length of the radius cannot be estimated.

Pelvis.—In the adult specimen (UCMP 123180) the distance between acetabulum and sacroiliac junction is short, so that the acetabulum would have been only a little below the sacrum. The acetabulum is deep, closed medially by an extremely thin wall of bone. Anterior to the acetabulum, and at about the same level as its ventral border, is a prominent tuberosity; dorsal to this tuberosity is a smaller one. These are probably for the origin of the M. rectus femoris, which acts with other parts of the quadriceps muscle to extend the knee. In the juvenile (UCMP 123181) the ilium is very flat but has a thickened midline. The anterior end curves slightly outward, and the epiphysis is only loosely fused. The ischium is low, flattened on the medial side. The dorsal lip of the acetabulum projects laterally well over the ventral rim. There is a deep acetabular notch. What is probably a small ischial spine lies just posterior to the acetabulum; ligaments of the hip joint attached here.

Femur.—The left femur (Fig. 5) of the adult (UCMP 123180) is the most complete limb bone known from either specimen, lacking only a few millimeters of the shaft. The greater trochanter is large, anteroposteriorly elongated, and separated from the head by a deep groove. The lesser trochanter is prominent and lies on the medial surface

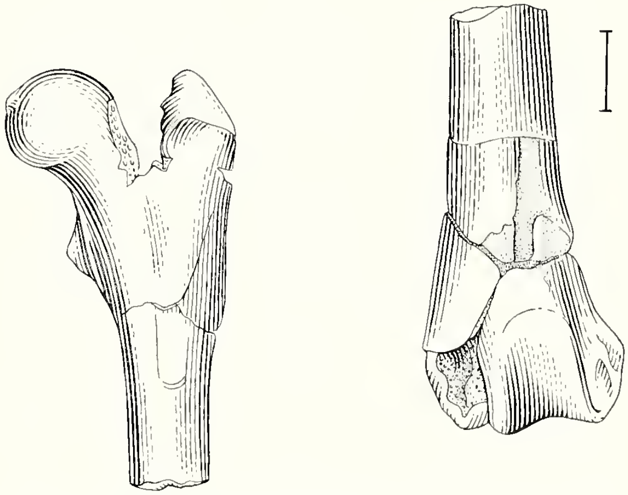

Fig. 5.—*Eusmilus cerebralis,* UCMP 123180. Left femur, anterior view. Scale bar equals 1 cm.

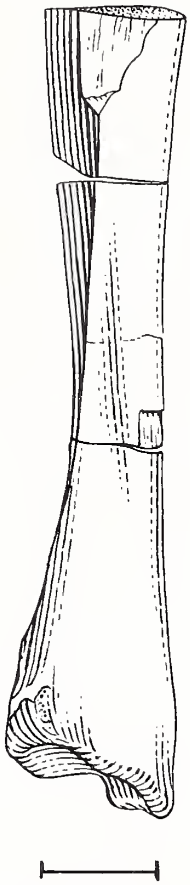

Fig. 6.—*Eusmilus cerebralis*, UCMP 123180. Left distal tibia, posterior view. Scale bar equals 1 cm.

of the shaft. In most living carnivores it lies more posteriorly. Opposite it, on the lateral surface of the shaft, is a prominent ridge extending from the greater trochanter to the large gluteal tuberosity or third trochanter (absent in felines) where the gluteus medius and part of the gluteus maximus probably inserted. These two prominences on opposite sides of the shaft accentuate its anteroposterior flattening.

Both the medial and lateral distal condyles are small and narrow. The narrow intercondylar fossa is round in outline at its distal end, and the patellar groove is wide and shallow.

The proximal end of the right femur of the juvenile (UCMP 123181) lacks the epiphyses but is generally similar to that of the adult. Strong greater and lesser trochanters and a gluteal tuberosity are present.

Tibia.—Subequal lateral and medial condyles, only slightly separated from each other by a poorly defined groove, occupy the proximal surface of the adult (UCMP 123180) tibia. The fibular facet is essentially an overturned continuation of the posterolateral border of the lateral condyle. The wide, rugose cnemial crest does not project far anteriorly. The shaft of the tibia is transversely flattened and marked by two sharp crests; one is the distal extension of the cnemial crest and curves smoothly toward the medial surface of the bone, where it disappears before reaching the medial malleolus. A second crest, marking the line of attachment to the fibula, extends along the lateral surface (Fig. 6). The distal fibular facet is small and essentially continuous with the lateral articular surface for the astragalus. The medial malleolus is large and extends distally far beyond the level of the lateral malleolus. It probably provided a large area of attachment for the deltoid ligament, which extends from it to the dorsal surface of the tarsals. The distal articular surface of the tibia is distinctly triangular in outline. The grooves of the astragalar facet are so shallow as to be almost flat. The distal surface slopes proximally toward the lateral side. In medial view the most distal centimeter of the tibia appears "bent" posteriorly.

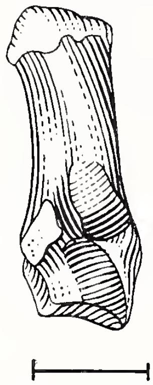

Fig. 7.—*Eusmilus cerebralis*, UCMP 123180. Left calcaneum, anterior view. Scale bar equals 1 cm.

I estimate the femorotibial index (tibia length/femur length × 100) for UCMP 123180 to be 94.1. Gonyea (1976) found that felids which occupy grasslands or open woodland have a high humeroradial index, that is, one appraoching or even exceeding 100, but apparently a high femorotibial index alone is not necessarily evidence of adaptation to open habitat. The fragmentary nature of the forelimb bones makes calculation or estimation of the humeroradial index for UCMP 123180 impossible. The high femorotibial index does, however, em-

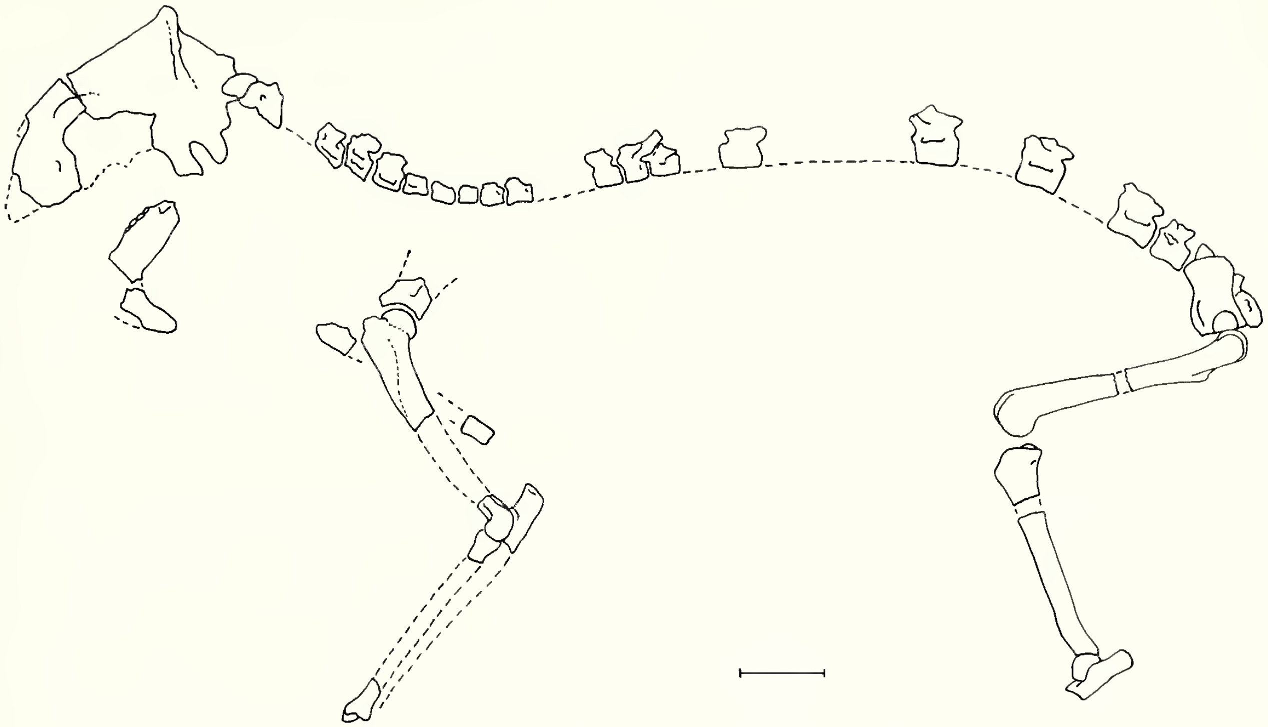

Fig. 8.—Reconstruction of the skeleton of *Eusmilus cerebralis*, UCMP 123180. Scale bar equals 5 cm.

phasize the differences in limb proportions between *Eusmilus cerebralis* and other sabertooths such as *Barbourofelis* and *Smilodon*, which had relatively short distal limb segments.

Astragalus.—The trochleae of the adult (UCMP 123180) astragalus are very flat and separated by a wide, shallow groove. The medial trochlea would have extended proximally across the medial surface of the calcaneum. The deeply excavated articulation for the fibula occupies the whole medial surface of the astragalus. A tiny astragalar foramen lies between the trochleae at their proximal ends. On the posterior surface are three facets for articulation with the calcaneum; a large, nearly vertical lateral facet, and the remnants of two medial facets. It is apparent from this that the portion of the sustentaculum tali missing from the calcaneum is extensive, and would have borne a second astragalar facet on its medial extension (see description of the calcaneum, below). The two small medial calcanear facets on the astragalus are oval in outline. The more proximal was apparently much the smaller, and the two are well separated. Between the medial and lateral facets is a deep groove for the interosseus ligament.

Calcaneum.—The left calcaneum (Fig. 7) of the adult (UCMP 123180) lacks only the medial extension of the sustentaculum tali. The proximal end of the calcaneum is an expanded knob of bone. The lateral articulation for the astragalus is narrow, begins high above the cuboid facet, and extends far up the shaft. What remains of the medial astragalar facet is also well separated from the cuboid facet. The plane of the cuboid facet lies not perpendicular to the axis of the calcaneum shaft but slants proximally toward the medial side, giving the distal end of the calcaneum a distinct point on the lateral side. The cuboid facet is small and oval, with no indication of a navicular facet medial to it.

ACKNOWLEDGMENTS

I wish to thank J. A. Robinson, J. H. Hutchison, and M. Morea for contributing both ideas and information during preparation of this manuscript. J. Peek and J. Clark spent hours X-raying the juvenile dentaries before preparation which exposed the teeth, but the material proved unyielding. J. P. Lufkin drew figures 1 through 7, and J. H. Hutchison assisted with the reconstruction of the adult skeleton, Fig. 8. M. O. Woodburne provided photographs of the type skull and jaws of *Eusmilus bidentatus*.

LITERATURE CITED

Baskin, J. A. 1981. *Barbourofelis* (Nimravidae) and *Nimravides* (Felidae) with a description of two new species from the late Miocene of Florida. J. Mamm., 62:122–139.

Cope, E. D. 1880. On the extinct cats of America. Amer. Nat., 14:833–858.

Gervais, P. 1876. Zoologie et paleontologie générales. Paris, 2^{e} ser., 72 pp.

Gonyea, W. J. 1976. Behavioral implications of saber-toothed felid morphology. Paleobiol., 2(4):332–342.

Hatcher, J. B. 1895. Discovery, in the Oligocene of South Dakota, of *Eusmilus*, a genus of sabre-toothed cats new to North America. Amer. Nat., 24:1091–1093.

Macdonald, J. R. 1963. The Miocene faunas from the Wounded Knee area of South Dakota. Bull. Amer. Mus. Nat. Hist., 125 (3):139–238.

———. 1970. A review of the Miocene Wounded Knee faunas of southwestern South Dakota. Bull. Nat. Hist. Mus. Los Angeles County, 8:1–82.

Martin, L. D. 1980. Functional morphology and the evolution of cats. Trans. Nebraska Acad. Sci., 8:141–154.

Radinsky, L. 1969. Outlines of canid and felid brain evolution. Ann. New York Acad. Sci., 67 (1):277–288.

———. 1971. An example of parallelism in carnivore brain evolution. Evolution, 23:518–522.

Stock, C. 1933. Carnivora from the Sespe of the Las Posas Hills, California. Carnegie Inst. Washington, Publ., 440:29–41.

Toohey, L. 1959. The species of *Nimravus* (Carnivora, Felidae). Bull. Amer. Mus. Nat. Hist., 118:73–112.

Address: Department of Paleontology, University of California, Berkeley, California 94720.
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A NEW CUCKOO AND A CHACHALACA FROM THE EARLY MIOCENE OF COLORADO

LARRY D. MARTIN AND ROBERT M. MENGEL

ABSTRACT

We report two fossil avian species from the early Miocene (Marslandian) of Logan County, Colorado. A terrestrial cuckoo, represented by part of a tarsometatarsus, coracoid, and carpometacarpus is described and named *Cursoricoccyx* (new genus) *geraldinae* (new species), and assigned to the Neomorphinae. It appears to be a close relative of the modern road runners (*Geococcyx*). In age it antedates all known, unequivocal cuckoos save *Neococcyx mccorquodalei* from the Oligocene of Saskatchewan. A partial right tibiotarsus of a chachalaca-like cracid is reported and discussed.

INTRODUCTION

Almost 20 years ago, Robert W. Wilson described the first extensive fauna of small vertebrates from the early Miocene (Hemingfordian) of North America (Wilson, 1960). This fauna, Martin Canyon A Local Fauna, is still incompletely known. Wilson restricted his efforts to the rodents and insectivores; further publications are available on the cryptobranchid salamanders (Meszoely, 1966) and some of the mammals (Galbreath, 1953; Black, 1963; Dawson, 1965; J. E. Martin, 1978; Yatkola and Tanner, 1979). The only reported avifauna that is close to the Martin Canyon A Local Fauna both chronologically and geographically is the Flint Hill Local Fauna in the Batesland Formation (Hemingfordian of South Dakota) reported by Miller (1944). We have begun to study some of the few birds thus far found in the Martin Canyon A Local Fauna and report in this paper on a cuculiform and a galliform from that fauna.

The faunal list from Martin Canyon A presently includes the following:

Amphechinus (hedgehog), *Plesiosorex* (insectivore); *Pseudotrimylus roperi* (Wilson), *P. compressus* (Wilson), *Angustidens vireti* (Wilson), and *Wilsonsorex conulatus* Martin (shrews); *Mydecodon martini* Wilson, *Scalopoides isodens* Wilson, and *Proscalops* (moles); *Oreolagus wilsoni* Dawson (pika), *Hypolagus*? sp. (rabbit); *Mesogaulus paniensis* Matthew (mylagaulid); *Miospermophilus bryanti* Wilson (ground squirrel); *Sciurus*? sp. (squirrels); *Anchitheriomys*? sp. (large beaver), *Monosaulax* sp. (small round-incisored beaver): *Pseudotheridomys hesperus* Wilson (eomyid); *Proheteromys* cf. *magnus* Wood, *Mookomys* cf. *formicorum* Wood, and *Florentiamys*? sp. (heteromyids); *Plesiosminthus clivosus* Galbreath and *Schaubeumys galbreathi* Wilson (sicistines); *Cynarctoides arcidens* (Barbour and Cook) and *Tomarctus* (canids); Amphicyonine sp.: *Parahippus pawniensis* Gidley (horse); *Brachypotherium americanus* Yatkola and Tanner (rhinoceros); *Hesperhys* (peccary); *Merycochoerus proprius* Loomis and *M. magnus* Loomis (oreodonts); *Oxydactylus* (*camel*); *and Barbouromeryx* (primitive cervid).

FAMILY CUCULIDAE

Three partial skeletal elements in the University of Kansas Museum of Natural History, Division of Vertebrate Paleontology (KUVP), a right tarsometatarsus, a right coracoid, and a left carpometacarpus from the Martin Canyon A Local Fauna are referable to the Cuculidae and are of a size and morphology compatible with conspecifieity. There is no way to determine whether they represent one, two, or three individuals.

The tarsometatarsus is represented by only the proximal end, but it shows the two subequal hypotarsal canals characteristic of the Cuculidae. The coracoid is represented by the humeral end with the elongated, strap-like procoracoid characteristic of the Cuculidae. The carpometacarpus is nearly complete, except that the distal end is separated by a small gap without contacts. The two pieces were found in direct association with each other. The carpometacarpus lacks a metacarpal process bridging the intermetacarpal space, which is broad. This is not so apparent in Fig. 1 because the third metacarpal has been broken and bent into the intermetacarpal space, but the correct width can be estimated by looking at the intermetacarpal symphysis on the distal end. Metacarpal III extends slightly distal to metacarpal II and has a smoothly rounded junction with the facet for digit III.

The following living cuculids (classification of Peters, 1940) were used in the comparisons: Cuculinae—*Cuculus canorus, Chalcites malayanus.* [According to Parker's revision (1981), which includes this species in *Chrysococcyx, Cuculus malayanus* (Raffles) 1822 is a junior synonym of *Cuculus xanthorhynchus* (Horsfield) 1821 and the next available name is *Chrysococcyx minutillus* Gould (see Peters, 1940, for sources).] Phaenicophaeinae—*Coccyzus americanus, Piaya cayana*; Crotophaginae—*Crotophaga sulcirostris*; Neomorphinae—*Tapera naevia, Morococcyx erythropygius, Geococcyx californianus, G. velox, Dromococcyx phasianellus, Neomorphus geoffroyi*; Centropodinae—*Centropus bengalensis.* No example of *Coua* (sometimes placed in a subfamily Couinae) was examined, but the differences noted of *Centropus,* in whose subfamily *Coua* is often placed, make it seem unlikely that this presently Madagascan genus has any relevance to neomorphine cuckoos.

The fossil differs from the Cuculinae in having the procoracoid slanting anteriorly and very narrow, and the carpometacarpus with metacarpal III more produced distally. (We consider the homology of digits in the avian manus still very much an open matter and lean toward the classic numbering I–II–III; this also accords with the now classic terminology of Howard [1929] which we follow.) The Centropodinae have tarsometatarsi with wider proximal ends, and shallow, narrow-rimmed anterior metatarsal grooves. They also have very broad procoracoids. Compared with the fossil, the Crotophaginae have the anterior metatarsal groove on the tarsometatarsus deeper, broader, and more narrowly rimmed, with the papilla for *M. tibialis anticus* indistinct, being situated far proximally and laterally. In the carpometacarpus, the intermetacarpal space is broader than in the fossil. The furcular facet of the crotophagine coracoid slants more anteriorly and the procoracoid is broader. The Phaenicophaeinae are also unlike the fossil, having the medial hypotarsal canal much larger than the lateral one, and the anterior metatarsal groove shallower, broader, and more excavated proximally. The papilla of *M. tibialis anticus* is on the medial side. The procoracoid is broad (narrower in the fossil). The fossil resembles *Geococcyx* of the Neomorphinae in having the anterior metatarsal depression relatively shallow and narrow, with the lateral edge thick, and the hypotarsal canals of about the same relative size. Both the fossil and *Geococcyx* have the furcular facet inclined posteriorly (differing in this respect from all other cuckoos used in the comparisons except for *Neomorphus geoffroyi*).

It therefore seems clear that the fossil is referable to the Neomorphinae and is rather closely related to the living roadrunners, *Geococcyx*. For the fossil we propose a new genus:

Cursoricoccyx, new genus

Genotypic species.—*Cursoricoccyx geraldinae* new species.

Diagnosis.—Hypotarsus joined to the lateral cotyla at almost a right angle (curved in *Geococcyx*); hypotarsal canals relatively small; coracoid with triossial canal relatively narrower than in *Geococcyx* and its brachial tuberosity not as extended medially; on the carpometacarpus, metacarpal III flat and broad but not so semilunate as in *Geococcyx*; lateral internal carpal trochlea much more distal than the internal carpal trochlea (nearly at the same level in *Geococcyx*). Tarsometatarsus with external cotyla relatively larger and postero-lateral edge of proximal end less flattened than in *Tapera.* Tarsometatarsus in *Neomorphus geoffroyi* unlike that of *Cursoricoccyx* in having large, penetrating proximal foramina, a broader anterior metatarsal groove (its proximal end in fact proportionally broader than in *Cursoricoccyx*), and the proximal end of the posterior metatarsal groove more deeply excavated medial to the hypotarsus; furcular facet of the coracoid extends farther from the shaft in *Neomorphus geoffroyi* than in *Cursoricoccyx.* Tarsometatarsus also broader proximally in *Dromococcyx phasianellus* than in *Cursoricoccyx,* and more deeply excavated medial to the hypotarsus; last character shared by *Morococcyx erythropygius,* which also differs from *Cursoricoccyx* in having the furcular facet projecting forward. Carpometacarpus seems relatively longer than in *Neomorphus geoffroyi, Dromococcyx phasianellus,* and *Morococcyx.*

Cursoricoccyx geraldinae, new species

Figs. 1, 2

Holotype.—Proximal end of a right tarsometatarsus, KUVP no. 25629, Fig. 2, B–F.

Type locality and horizon.—Martin Canyon Local Fauna, Quarry A, in the NE ¼ sec. 27, T11N, R53W, Logan County, Colorado. The horizon is in

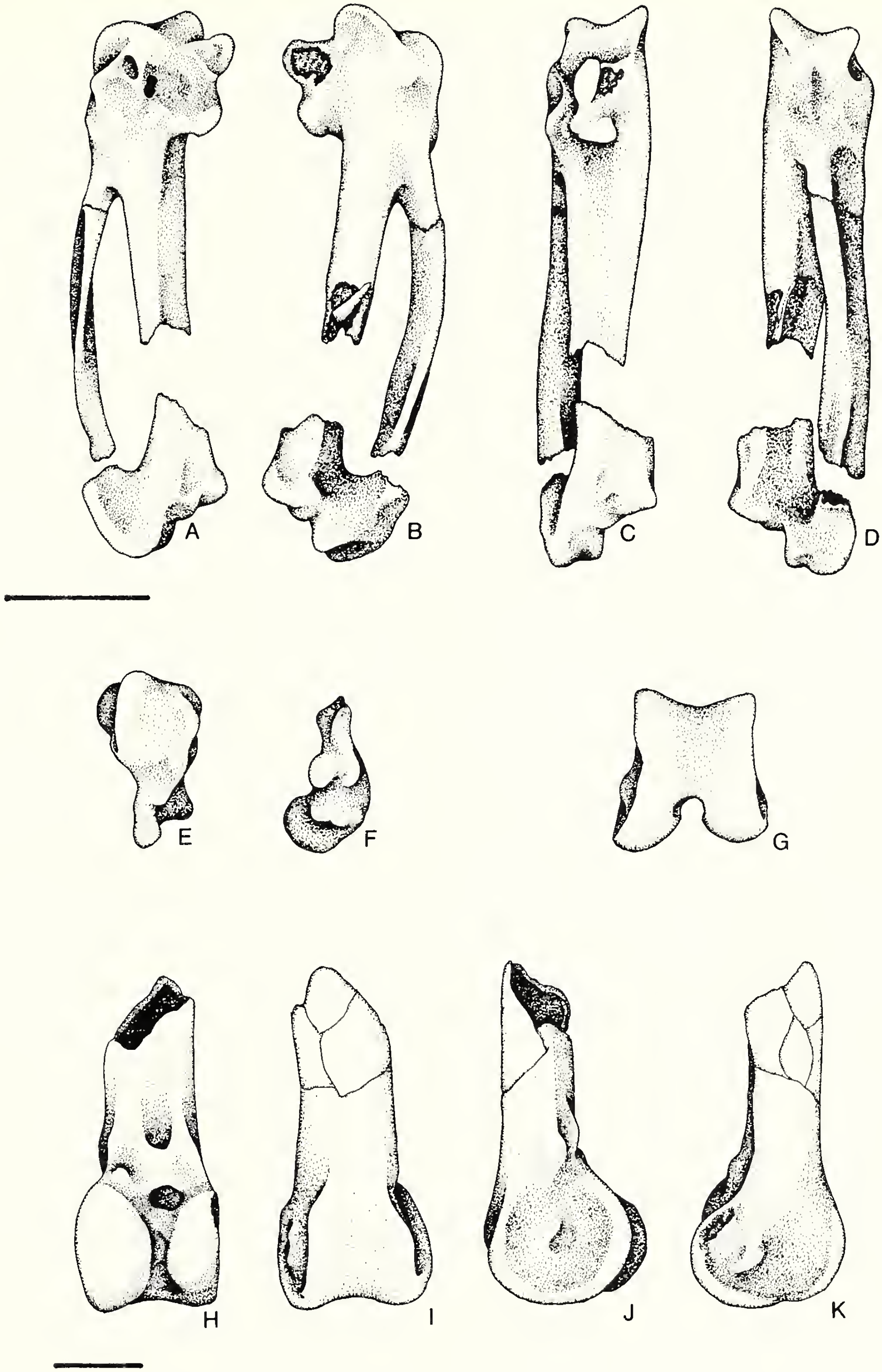

Fig. 1.—*Cursoricoccyx geraldinae,* A–F. Left carpometacarpus, KUVP 25631, internal, external, anterior, posterior, proximal, and distal views. Cracid, genus and species indeterminate, G–K. Distal end of right tibiotarsus, KUVP 9901, distal, anterior, posterior, lateral, and medial views. Bars = approximately 5 mm.

the Pawnee Creek Formation (Marslandian; early Miocene).

Diagnosis.—As for the genus.

Description.—A cuculid slightly smaller than living *Geococcyx velox.* The proximal end of the tarsometatarsus is damaged in the area of the proximal foramina, which, however, were evidently situated proximally, almost centered on the shaft, and very close together. The anterior metatarsal groove extends farther proximally than in *Geococcyx,* and is shallower than in *Crotophaga.* The anterior metatarsal groove is shallow and made narrow by the thickened lateral margin of the shaft (also found in *Geococcyx* but not in most other cuculids). The proximal ligamental attachment is not as prominent as in *Geococcyx* and the intercotylar prominence is broad and occupies almost all of the intercotylar area, although it is not as large and blunt as it is in *Crotophaga.* The internal cotyla is more rounded than in *Geococcyx* and the anterior margin of the external cotyla is straight (not extending anteriorly as in *Geococcyx*). Posterior to the internal cotyla is a small facet which is elongated from side to side in *Cursoricoccyx* and *Geococcyx,* but is elongated from front to back in most other cuculids. The hypotarsis in *Cursoricoccyx* is not as excavated medially as in *Geococcyx.*

The coracoid (KUVP no. 25630) is slender and has a long, strap-like procoracoid. The tip of the procoracoid process is eroded but is unlikely to have been much longer. It is not inclined as far ventrally as in *Geococcyx* but is similarly inclined anteriorly. The furcular facet is not cupped and is inclined anteriorly more than in *Geococcyx.* The glenoid facet is narrow and blends into the coraco-humeral surface. The area of the furcular facet is large and depressed. The coraco-humeral surface is not as curved dorsally as in *Geococcyx.*

The carpometacarpus (KUVP no. 25631) has the minor metacarpal (III) bowed so that the intermetacarpal space is relatively broad. This is masked by a break near the proximal end of metacarpal III, which resulted in its being deformed into the intermetacarpal space. Metacarpal III is broad and grooved on its internal anterior edge. The intermetacarpal tuberosity is not readily identifiable. The internal carpal trochlea is much more distal than the proximal one (about the same level as in *Geococcyx*). The process of the alular metacarpal (I) is narrower and more triangular in *Cursoricoccyx* than in *Geococcyx* and is turned more proximally. The ligamental attachment of the pisiform process is less developed than in *Geococcyx.* The pollical facet of *Cursoricoccyx* is on a prominent knob that is as large as the process of metacarpal I itself. The extension attachment on the alular metacarpal is small and oval (larger than in *Geococcyx*). The internal trochlea on the proximal end is not rounded as in *Geococcyx* and the external ligamental attachment on the proximal end is very large, rounded, and centered on the shaft of the major metacarpal (II).

The facet for the minor digit (III) extends slightly distal to the facet for digit II as it does in *Geococcyx.* Facet for digit II shaped much as in *G. californianus* but more rounded posteriorly. Metacarpal III produced more as an edge from the facet for digit III, which it enters as a smooth curve as in the other roadrunners.

Measurements.—Holotype, KUVP 25629, proximal tarsometatarsus: transverse width, 5.4 mm; anteroposterior diameter of external cotyla, 3.7 mm, and of internal cotyla, 3.0 mm. Carpometacarpus (KUVP 25631), greatest width of distal end (across the pisiform process), 6.0 mm. Coracoid (KUVP 25630), height of humeral end above scapular facet, 6.2 mm.

Etymology.—Adjectival combining form derived from the Latin noun *Cursor,* a runner, plus *coccyx,* Latinized form of the Greek word for cuckoo. The modifying specific name *geraldinae* honors the late Geraldine Lee Wilson (Mrs. Robert W.) who was pleased and amused by the promise of this recognition.

Discussion.—*Cursoricoccyx* and *Neococcyx* are presently the only cuculids yet described from the Tertiary (see Brodkorb, 1971). The oldest known cuculid is *Neococcyx mccorquodalei* Weigel (1963) from the lower Oligocene Cypress Hills Local Fauna in Saskatchewan, Canada. Brodkorb (1971:204) placed *Neococcyx* in his subfamily Coccyginae (= Phaenicophaeinae of Peters, 1940:41, and this paper). Reports of cuculids from the Eocene appear to be in error. These include *Uintornis* Marsh from the middle Eocene of Wyoming, which was referred to the Cuculidae by Cracraft and Moroney (1969) followed by Brodkorb (1970; 1971). Feduccia and Martin (1976) argued instead that *Uintornis* was a member of the extinct family Primobucconidae, presently placed in the Piciformes. Harrison and Walker (1977) named *Parvicuculus minor* from the lower Eocene of England and assigned it to the Cuculidae. Olson and Feduccia (1979) later assigned this taxon to the Primobucconidae. While we would agree that *Parvicuculus* is not a cuculid, examination of the holotype by L. Martin revealed that the troch-

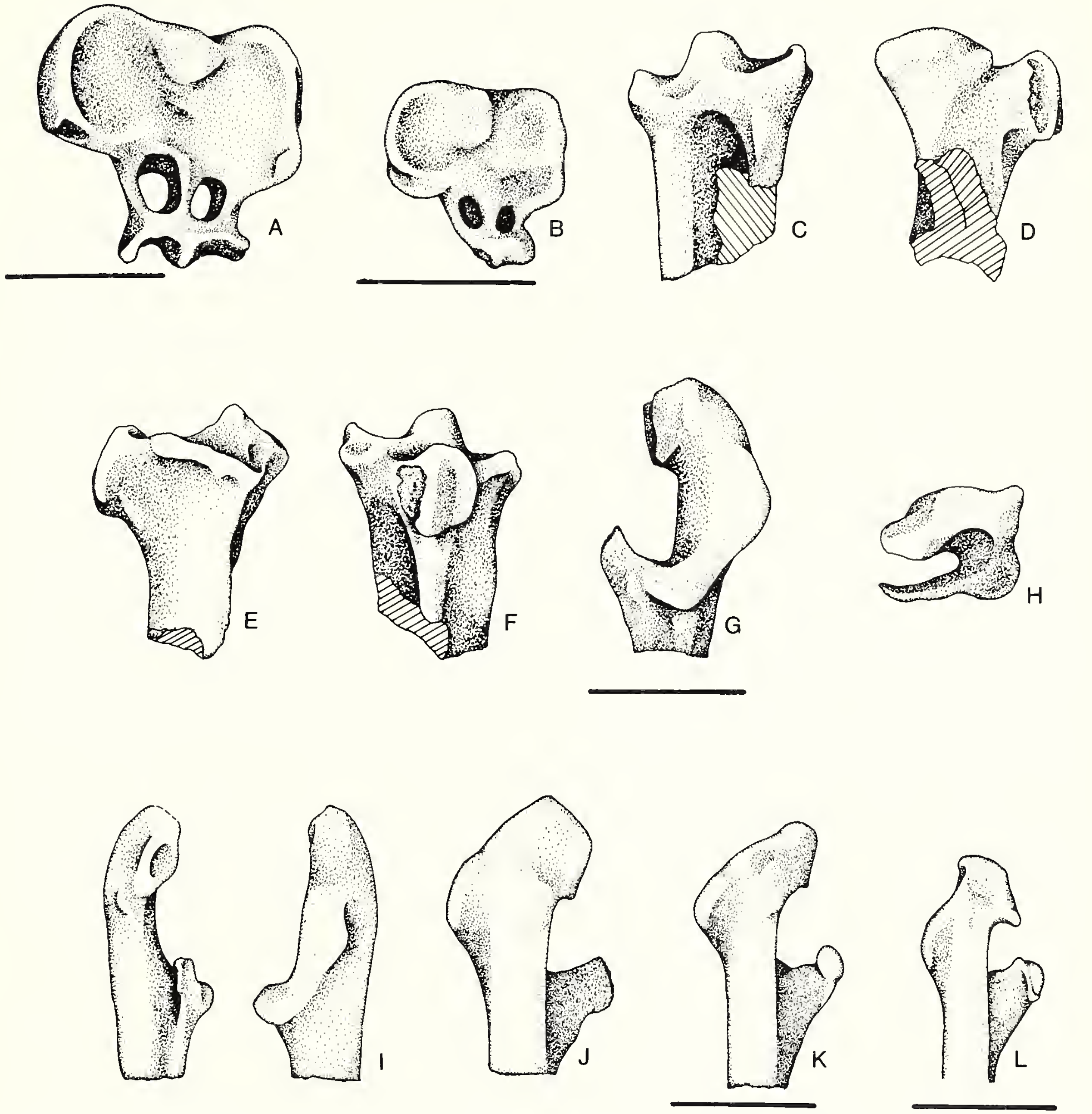

Fig. 2.—*Geococcyx californianus,* A. Proximal view of right tarsometatarsus. *Cursoricoccyx geraldinae,* B–F. Proximal end of right tarsometatarsus, KUVP 25629 (holotype), proximal, anterior, medial, lateral, and posterior views; G–J, humeral end of right coracoid, KUVP 25630, dorsal, distal, medial, lateral, and ventral views. *Geococcyx californianus,* K. Humeral end of right coracoid, ventral view. *Coccyzus americanus,* L. Humeral end of right coracoid, ventral view. Bars = approximately 5 mm.

leae are not nearly in a straight line as in the primobucconids, which have the middle trochlea only a little produced anteriorly. It also differs from the primobucconids in having the outer trochlea small, not deeply grooved and not turned medially, and it does not have a posteriorly projecting flange. Neither does it have two enclosed tendinal canals in the hypotarsus as do all of the Cuculidae we have examined. Martin does not think that it is a primobucconid, although assignment to the Coraciiformes would not be unlikely. We agree with Olson and Feduccia's (1979) statement that *Procuculus mi-*

nutus Harrison and Walker cannot be assigned either to the Cuculidae or the Primobucconidae.

The only other extinct neomorphine cuculid yet described is *Geococcyx conklingi* Howard from the late Pleistocene of New Mexico and Mexico. It is distinctly larger than *Geococcyx californianus,* but is otherwise similar to it (Howard, 1931) and does not warrant detailed comparison with *Cursoricoccyx.*

FAMILY CRACIDAE

A distal right tibiotarsus from the Martin Canyon A Local Fauna appears to be cracid but differs from all previously known species of the family represented by the tibiotarsus, Fig. 1, G–K.

Cracidae, genus, and species indeterminate

Material.—Distal end of right tibiotarsus, KUVP no. 9901.

Locality and horizon.—Martin Canyon Local Fauna, Quarry A, in the NE ¼ sec. 27, T11N, R53W, Logan County, Colorado; Pawnee Creek Formation (Marslandian; early Miocene).

Description.—The right tibiotarsus of a cracid about the size of living *Ortalis vetula* (Wagler), or slightly smaller, but with the distal end compressed, the tendinal groove narrower, and the supratendinal bridge narrower than in the Recent species. Resembles *Boreortalis* Brodkorb and differs from all other cracids for which the tibiotarsus is known in having the external condyle extending less abruptly forward from the shaft. Smaller than *B. laesslei* Brodkorb and *B. pollocaris* (Miller) and larger than *B. tedfordi* (Miller), *B. tantala* (Wetmore), and *B. phengites* (Wetmore). The groove for *M. peroneus profundus* is well defined and lateral. The tubercle on the supratendinal bridge is more lateral than in *B. laesslei.* The distal margin of the anterior intercotylar fossa bears a small, deep pit in *Ortalis,* which is not well defined in the present fossil or in *B. laesslei.* In the present fossil the internal condyle is less rounded and relatively thicker than in *Ortalis,* and its posterior intercondylar sulcus grades less abruptly to the shaft than in *Ortalis.*

Measurements.—KUVP 9901, distal end of tibiotarsus: transverse width, 8.2 mm; anteroposterior width, 8.4 mm.

Discussion.—*Boreortalis laesslei* is probably close to the same age as the Martin Canyon A specimen. Although it differs from the latter in several important characters, the shape of the external condyle suggests that they might be placed in the same genus. In *B. tantala* this feature is not so evident and assignment of that form to this genus is not certain (Brodkorb, 1954:181). Additional material of *B. laesslei* apparently has been found (Brodkorb, 1964), but until it is described the generic assignment of Tertiary cracids not represented by tibiotarsi must be regarded as tentative.

The usefulness of the tibiotarsus in paleo-ornithology varies among taxonomic groups and the estimation of its over-all value from one worker to another. David W. Steadman (pers. comm.) actually hates them.

A particular problem with galliforms is that their early history has not been worked out. Many of the characters we now think of as characterizing cracids may in fact simply be primitive galliform features, which have persisted in modern cracids but which may also have been present in other galliforms in the Tertiary.

Cracids today are Neotropical birds. A fairly large number of presumed cracids has been described from North America throughout the Tertiary and this is probably a reflection of the generally subtropical conditions that extended into very high latitudes during much of that time (Schultz et al., 1975).

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LITERATURE CITED

Black, C. C. 1963. A review of the North American Sciuridae. Bull. Mus. Comp. Zool., Harvard Univ., 130(3):1–248.

Brodkorb, P. 1954. A chachalaca from the Miocene of Florida. Wilson Bull., 66:180–183.

———. 1964. Catalogue of fossil birds. Part 2 (Anseriformes through Galliformes). Bull. Florida St. Mus., 8(3):195–335.

———. 1970. An Eocene puffbird from Wyoming. Univ. Wyoming Contrib. Geol., 9(1):13–15.

———. 1971. Catalogue of fossil birds. Part 4 (Columbiformes through Piciformes). Bull. Florida St. Mus., 15(4):163–266.

Cracraft, J., and J. J. Moroney, Jr. 1969. A new Pliocene woodpecker, with comments on the fossil Picidae. Amer. Mus. Novit., no. 2400:1–8.

Dawson, M. R. 1965. *Oreolagus* and other Lagomorphs (Mammalia) from the Miocene of Colorado, Wyoming, and Oregon. Univ. Colorado Studies Series, Earth Sci., 1:1–36.

Feduccia, J. A., and L. D. Martin. 1976. The Eocene zygodactyl birds of North America (Aves: Piciformes). Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore (S. Olson, ed.). Smithsonian Contrib. Paleobiol., 27:101–110.

Feduccia, J. A., and R. L. Wilson. 1967. Avian fossils from the lower Pliocene of Kansas. Occas. Papers Mus. Zool., Univ. Michigan, 655:1–6.

Galbreath, E. C. 1953. A contribution to the Tertiary geology and paleontology of northeastern Colorado. Univ. Kansas Paleont. Contrib., Vertebrata, 4:1–120.

Harrison, C. J. O., and C. A. Walker. 1977. Birds of the British lower Eocene. Tertiary Res. Spec. Paper, 3:1–52.

Howard, H. 1929. The avifauna of Emeryville Shellmound. Univ. California Publs. Zool., 32(2):301–394. (See also Contrib. Sci. Nat. Hist. Mus. Los Angeles County, 1980, no. 330: xxvii–xxxviii.)

———. 1931. A new species of roadrunner from Quaternary cave deposits in New Mexico. Condor, 33:206–209.

Martin, J. E. 1978. A new and unusual shrew (Soricidae) from the Miocene of Colorado and South Dakota. J. Paleont., 52: 636–641.

Meszoely, C. 1966. North American fossil cryptobranchid salamanders. Amer. Midl. Nat., 75:495–515.

Miller, A. H. 1944. An avifauna from the lower Miocene of South Dakota. Univ. California Publ., Bull. Dept. Geol. Sci., 27:85–99.

Olson, S. L., and J. A. Feduccia. 1979. An Old World occurrence of the Eocene avian family Primobucconidae. Proc. Biol. Soc. Washington, 92:494–497.

Parker, S. A. 1981. Prolegomenon to further studies in the Chrysococcyx 'Malayanus' group (Aves, Cuculidae). Zoologische Verhandelingen Rijksmus. Natuurl. Hist. Leiden. No. 187:1–560.

Peters, J. L. 1940. Checklist of birds of the world. Cambridge, Harvard Univ. Press, vol. 4.

Schultz, C. B., L. D. Martin, and R. G. Corner. 1975. Middle and late Cenozoic tapirs from Nebraska. Bull. Univ. Nebraska State Mus., 10 (no. 1, part 1):1–21.

Weigel, R. D. 1963. Oligocene birds from Saskatchewan. Quart. J. Florida Acad. Sci., 26:257–262.

Wilson, R. W. 1960. Early Miocene rodents and insectivores from northeastern Colorado. Univ. Kansas Paleont. Contrib., Vertebrata, 7:1–92.

Yatkola, D., and L. G. Tanner. 1979. *Brachypotherium* from the Tertiary of North America. Univ. Kansas Mus. Nat. Hist., Occas. Papers, 77:1–11.

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A NEW SPECIES OF XENACANTHODII (CHONDRICHTHYES, ELASMOBRANCHII) FROM THE LATE PENNSYLVANIAN OF NEBRASKA

Gary D. Johnson

ABSTRACT

Isolated teeth from an unnamed sandstone in the Towle Shale Formation, Late Pennsylvanian, Virgilian (Stephanian B or C) of southeastern Nebraska comprise a new species of xenacanthodiid shark, *Xenacanthus*? *nebraskensis.* Generic characters include an apical button that is not isolated from the principal cusps. These cusps bear multiple cristae and their distal ends are cylindrical rather than compressed. The angle between the major transverse axis of the proximal portion of the principal cusps and labial root margin is high. Differences from other species of *Xenacanthus* include the presence of cristae on the intermediate cusp with a pattern similar to that on the principal cusps; the intermediate cusp is proximally compressed; and the cristae extend onto the labial margin of the root. This species may belong to the Middle Paleozoic genus *Thrinacodus,* which possesses a cristated intermediate cusp; the position of the apical button is presently unknown for *Thrinacodus.*

INTRODUCTION

Xenacanthodiid sharks are known from the Late Devonian through the Late Triassic (Johnson, 1979, 1980), principally from isolated teeth and cephalic spines. *Orthacanthus* and *Xenacanthus* are known from skeletal remains as well (Fritsch, 1889, 1895; Johnson, 1979). I regard only one other genus, *Thrinacodus,* known from a few isolated teeth of Late Devonian and Mississippian age, as a valid taxon. Other unnamed genera, also known from isolated teeth, may have existed (Johnson, 1979); one was a contemporary of *Thrinacodus,* and two others may have been intermediate between these early genera and *Orthacanthus* and *Xenacanthus* which appeared later.

All xenacanthodiid teeth consist of a single root bearing a single apical button situated on the lingual side of the oral surface and a single tubercle situated on the labial side of the aboral (=basal) surface. The crown consists of two principal cusps protruding from the labial margin of the oral surface. One or more smaller cusps may occur between the principal cusps. See Hotton (1952) for a description of the mode of tooth replacement, which is most likely similar to that of modern elasmobranchs. The terms root and crown are used here in a loose sense, for convenience, since strictly speaking they occur only in mammalian teeth (Peyer, 1968:13–14).

The three named genera can be distinguished by differences in tooth morphology that are discussed at length in my review of the Xenacanthodii (Johnson, 1979). Briefly, *Orthacanthus* teeth have an apical button isolated from the principal cusps, which are compressed throughout their length; these cusps are smooth (without cristae) and usually carinated, and the carinae may be serrated; the major transverse axis of the proximal portion of the principal cusps (as seen in cross-section) forms a relatively low angle with the labial margin of the root; a variable number of intermediate cusps may be present; species assigned to this genus display considerable heterodonty in their dentitions. In *Xenacanthus* teeth the apical button is not isolated, but extends between the principal cusps; the distal ends of these cusps are more or less cylindrical and bear multiple cristae; the angle between the major transverse axis of the proximal portion of the principal cusps and labial root margin is relatively high; a single, usually smooth intermediate cusp may be present (absent in one species); species assigned to this genus have essentially homodont dentitions. Some species I provisionally assigned to *Xenacanthus* allegedly have smooth cusps; however, there is reason to believe that this may not be a valid character (Johnson, 1979, 1980). If it is a valid character, then these species may represent another unnamed genus.

I have assumed *Thrinacodus* to be a valid genus based only on a review of the literature (Johnson, 1979). Not all of the characters that might be used to distinguish it from other genera have been adequately described. St. John and Worthen (1875) described the principal and intermediate cusps of *T. nanus* as acutely pointed, so presumably they were more cylindrical than compressed, as in *Xenacanthus.* The major transverse axis of the proximal end of the principal cusps appears to be at a distinct angle to the labial margin of the root. The enlarged intermediate cusp is cristate. Unfortunately, the position of the apical button is unknown to me. The view of "*Diplodus*" *incurvus* given by Newberry and Worthen (1866, Pl. 4, fig. 4a) shows what may be the apical button at the lingual end of the root, well isolated from the cusps. Since St. John and Worthen (1875) incorporated this species into *Thrinacodus,* then it *might* be assumed that *T. nanus* also possessed an isolated apical button. However, examination of 21 specimens from the St. John/Springer Collection (National Museum of Natural History, NMNH 14897, 14909, and 15622) assigned to *D. incurvus* shows that they are not xenacanthodiid teeth. They very closely resemble Newberry and Worthen's (1866) illustration. They will be discussed in a future publication. Since the presence of an isolated apical button is unlike the situation in *Xenacanthus* species, then *Thrinacodus* may be a valid taxon. The most important feature of *Thrinacodus,* in view of its geologic age, is the combination of a single apical button and basal tubercle with a cristate intermediate cusp. In slightly older species of the form genus *Phoebodus,* the apical button and basal tubercle are elongate and appear to have developed from the fusion of paired structures, which occur on cladodont teeth of similar age (all of these teeth have cristate cusps; see Eastman, 1899; Johnson, 1979).

The descriptive terminology used here is discussed elsewhere (Johnson, 1979; Hotton, 1952); the central foramen is an enlarged opening that occurs between the principal cusps in many xenacanthodiid species. The method used to measure the teeth described below, and the reliability of these measurements are described elsewhere (Johnson, 1979). The anteromedial-posterolateral (am-pl) and labio-lingual (l-l) dimensions (length and width, respectively) are shown in Fig. 1. The abbreviation am/pl is used to denote both the am and pl margins of the teeth, since they cannot be differentiated.

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SYSTEMATIC ACCOUNT

Class Chondrichthyes
Subclass Elasmobranchii
Order Xenacanthodii (=Pleuracanthodii)
Family Xenacanthidae Fritsch, 1889

Xenacanthus Beyrich, 1848
***Xenacanthus*? *nebraskensis*,** new species
(Figs. 1–14)

Holotype.—TMM 41647-328, isolated tooth.

Paratypes.—TMM 41647-20, -21; TMM 41647-323–41647-327; TMM 41648-136–41648-140; all are isolated teeth.

Hypodigm.—Holotype, paratypes and TMM 41647-22 (178 isolated teeth from Site 2) and TMM 41648-14, -141 (59 isolated teeth from Site 3).

Repository.—Texas Memorial Museum, University of Texas, Austin (TMM).

Etymology.—Named for the state of Nebraska.

Locality.—Ossian's (1974) Peru locality, Sites 2 and 3, south of Peru, Nemaha County, Nebraska.

Age.—An unnamed sandstone in the Towle Shale Formation; Late Pennsylvanian, Virgilian (Stephanian B or C).

Diagnosis.—Labio-lingual and anteromedial-posterolateral root dimensions nearly equal. Prominent apical button separate from lingual margin but in contact with the intermediate cusp; central foramen absent. Basal tubercle with distinct labial margin, otherwise subdued, with a concave to flat articular surface. Principal cusps cylindrical, but compressed proximally, slightly divergent apically, sometimes recurved lingually. Cristae prominent, with six primary ones per cusp, usually extending full length of the cusps and onto the labial margin of the root; most originate at the distal end of the cusps, curving only slightly on the labial margin, the pattern often becoming random near the labial margin of the root; usually absent from lingual margin, but accompanied by shorter secondary cristae. Single, relatively large intermediate cusp always pres-

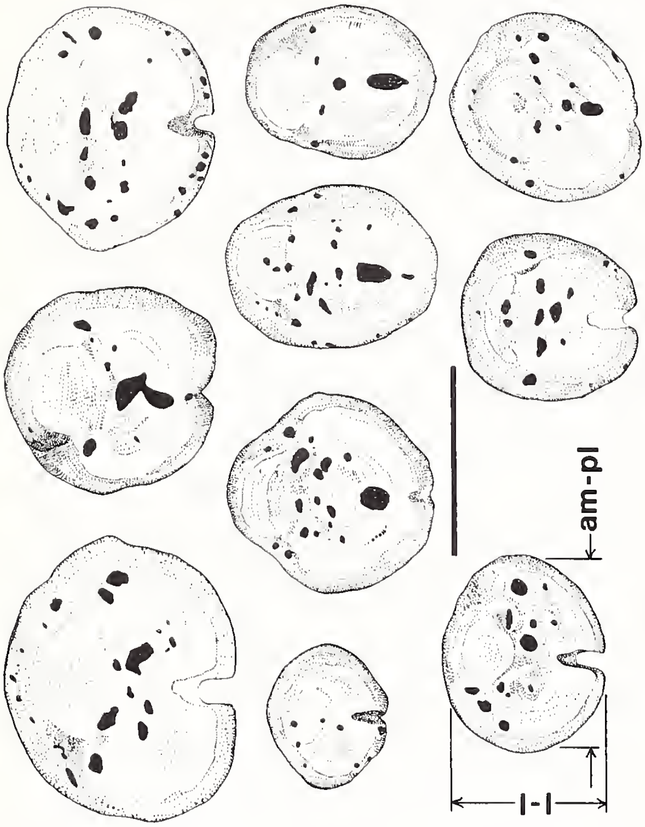

Fig. 1.—Root sketches of *Xenacanthus*? *nebraskensis*, new species, teeth from Site 3 of the Peru local fauna. Dimensional terms explained in text. Scale bar represents 1 mm.

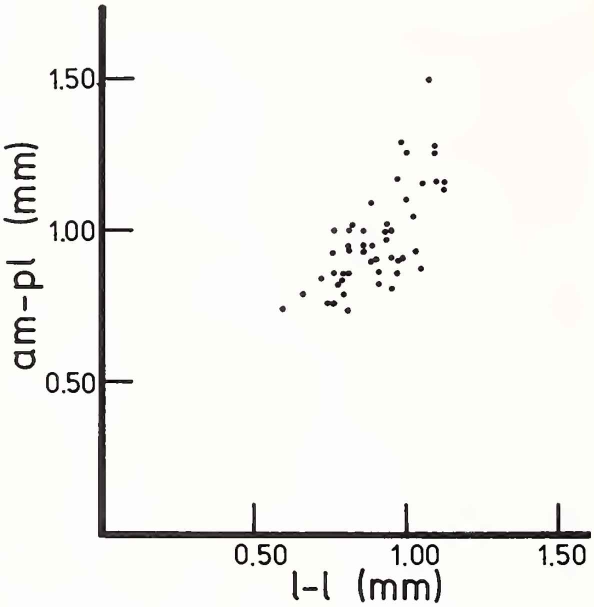

Fig. 2.—Measurements of 50 *Xenacanthus*? *nebraskensis*, new species, teeth from Site 3 of the Peru local fauna. See Fig. 1 and text for explanation of abbreviations. ranges = 0.59–1.12 (l-l) and 0.74–1.50 (am-pl); means ±1 SD. = 0.90 ± .13 (l-l) and 0.97 ± .16 (am-pl); a linear regression analysis (with confidence limits; see Simpson et al., 1960) gives a slope of 0.92 ± .27 and a y-intercept of +0.14 ± .24.

ent; it is cylindrical, but with proximal region distinctly compressed in anteromedial-posterolateral direction; cristate, with pattern similar to that of principal cusps.

Description.—The mean am-pl length of the root is slightly greater than the mean l-l width (Fig. 2). The apical button is always in contact with the intermediate cusp (Figs. 3–14). It is bulbous-looking, but has a tendency for its lingual edge to blend in with the root, giving the appearance of actually reaching the lingual margin of the root (Fig. 3). It is rarely penetrated by foramina, except in the lingual portion of the root. Foramina are usually absent in the vicinity of the cusps, but very small ones probably occur under the reduced shelflike overhang of the apical button near the principal cusps. The foramina in the base of the root are as randomly placed (Fig. 1) as in other xenacanthodiid species (Johnson, 1979), except for one consistency. An elongate (l-l) foramen always occurs along the midline at the lingual margin, penetrating the root just lingual of the apical button (Fig. 3a–e). In most instances it splits the margin to give the root a bifurcated appearance (Fig. 10a). The labial edge of the basal tubercle is well defined. The opposite edge may be distinct, or may grade into the base of the root. The base of the root is flat or slightly concave.

Compared with the root size, the principal cusps are rather short, giving the teeth a stout appearance (Figs. 3–14). The proximal ends of these cusps are compressed in a manner similar to the other *Xenacanthus* species, with the major transverse axis forming a sharp angle with the labial margin of the

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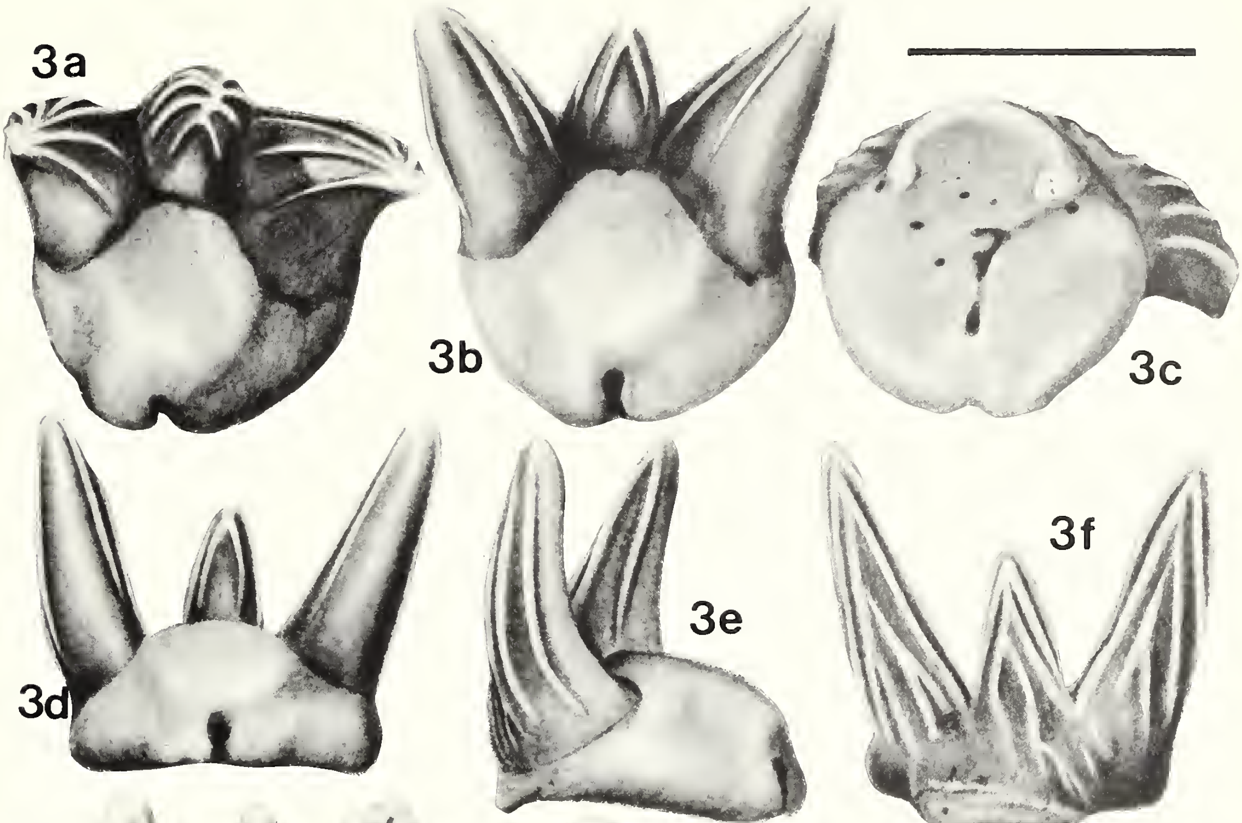
Figs. 3–5.—*Xenacanthus*? *nebraskensis*, new species, teeth from Site 2, Peru local fauna; scale bar represents 1 mm. Fig. 3.—TMM 41647-328, holotype: a, occlusal, b, lingual-occlusal, c, basal, d, lingual, e, am/pl, and f, labial views. Fig. 4.—TMM 41647-324, paratype: a, lingual-occlusal, b, am/pl, and c, labial views. Fig. 5.—TMM 41647-323, paratype: a, lingual-occlusal, b, am/pl, and c, labial views. 38×.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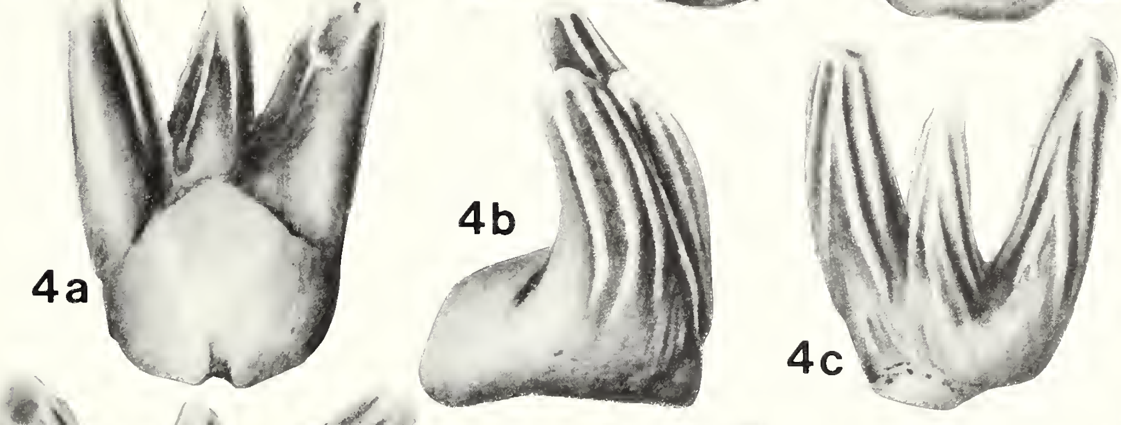
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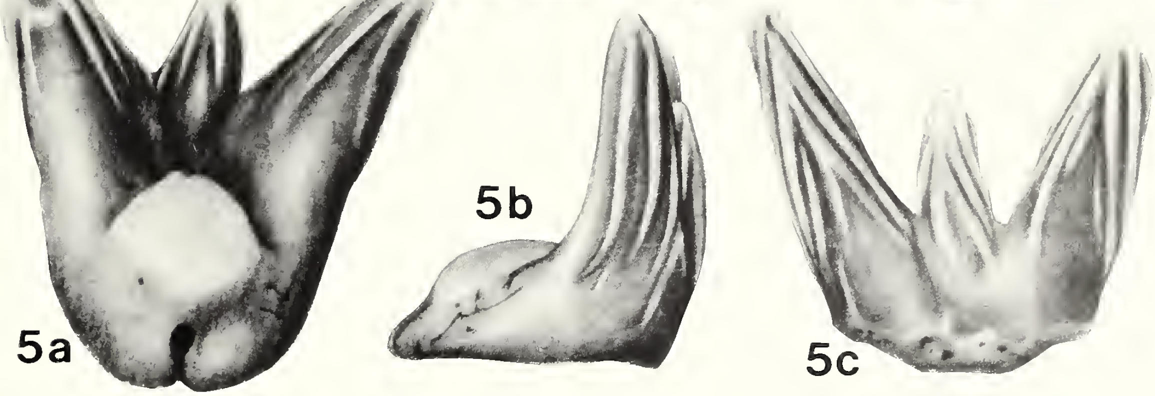
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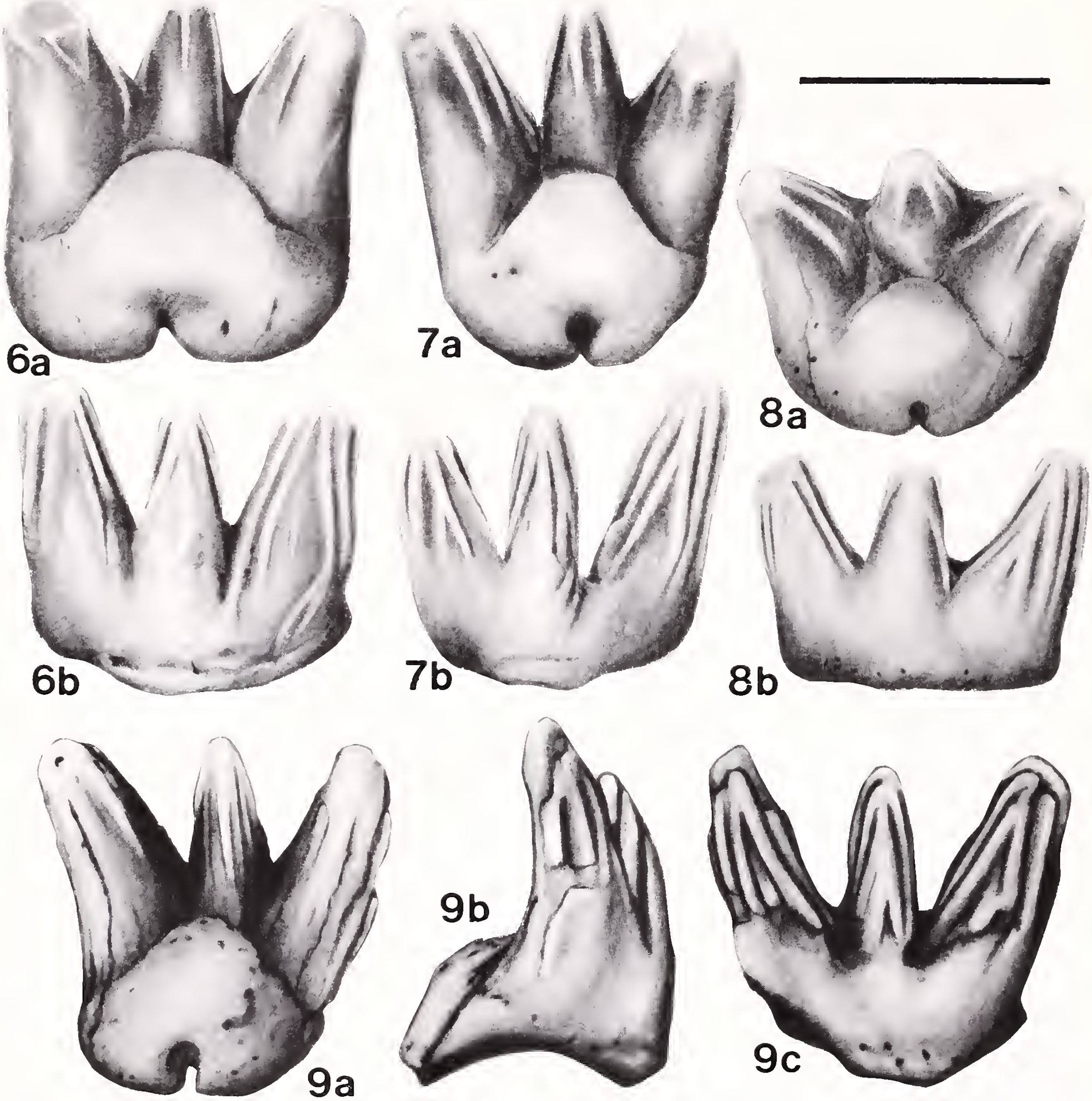


Figs. 6–9.—*Xenacanthus*? *nebraskensis*, new species, teeth from Site 2, Peru local fauna; scale bar represents 1 mm. Fig. 6.—TMM 41647-327, paratype: a, lingual-occlusal, and b, labial views. Fig. 7.—TMM 41647-326, paratype: a, lingual-occlusal, and b, labial views. Fig. 8.—TMM 41647-325, paratype: a, lingual-occlusal, and b, labial views. Fig. 9.—TMM 41647-20, paratype: a, lingual-occlusal, b, am/pl, and c, labial views. 38×.

root below the intermediate cusp. The cusps are of equal size, or very nearly so. They usually are slightly divergent but are occasionally vertical and parallel to one another. They are generally straight, but may be slightly recurved lingually. The stoutness of the intermediate cusp, combined with the fact that it reaches two thirds or more of the height of the principal cusps (or may even equal their height), contribute to the stout appearance of the teeth.

The pattern of the cristae may vary somewhat between the proximal regions of the principal cusps and the corresponding root margin of the same tooth

(Figs. 3–14). There are typically six cristae per cusp, with additional shorter ones occurring in the proximal region. Two slightly divergent pairs of cristae start on the labial margin of the tip accompanied by a single crista on each of the medial and am/pl margins. Those on the labial margin may be straight (Fig. 8b), or spiral slightly toward the medial and am/pl margins (Figs. 3, 12), sometimes recurving back toward the labial margin as they approach the root (Fig. 6b). Those occurring on the medial and am/pl margins tend to parallel the axis of the cusp (Fig. 3e). This general pattern occurs on the intermediate cusp as well as on the principal cusps. One of the cristae occurring nearest an imaginary center line on the labial margin of the principal cusps, or one on each side of this line, may be bifurcated in the proximal region (Figs. 3f, 6b). A single, shorter crista may occur in the proximal region of the labial margin (Fig. 6b). These additional cristae also occasionally occur on the intermediate cusp.

A pair of additional, rather fine cristae have been observed on the lingual margins of some of the principal cusps. A similar pair may be present on the intermediate cusp as well. These cristae do not extend the full length of any of the cusps (Fig. 7).

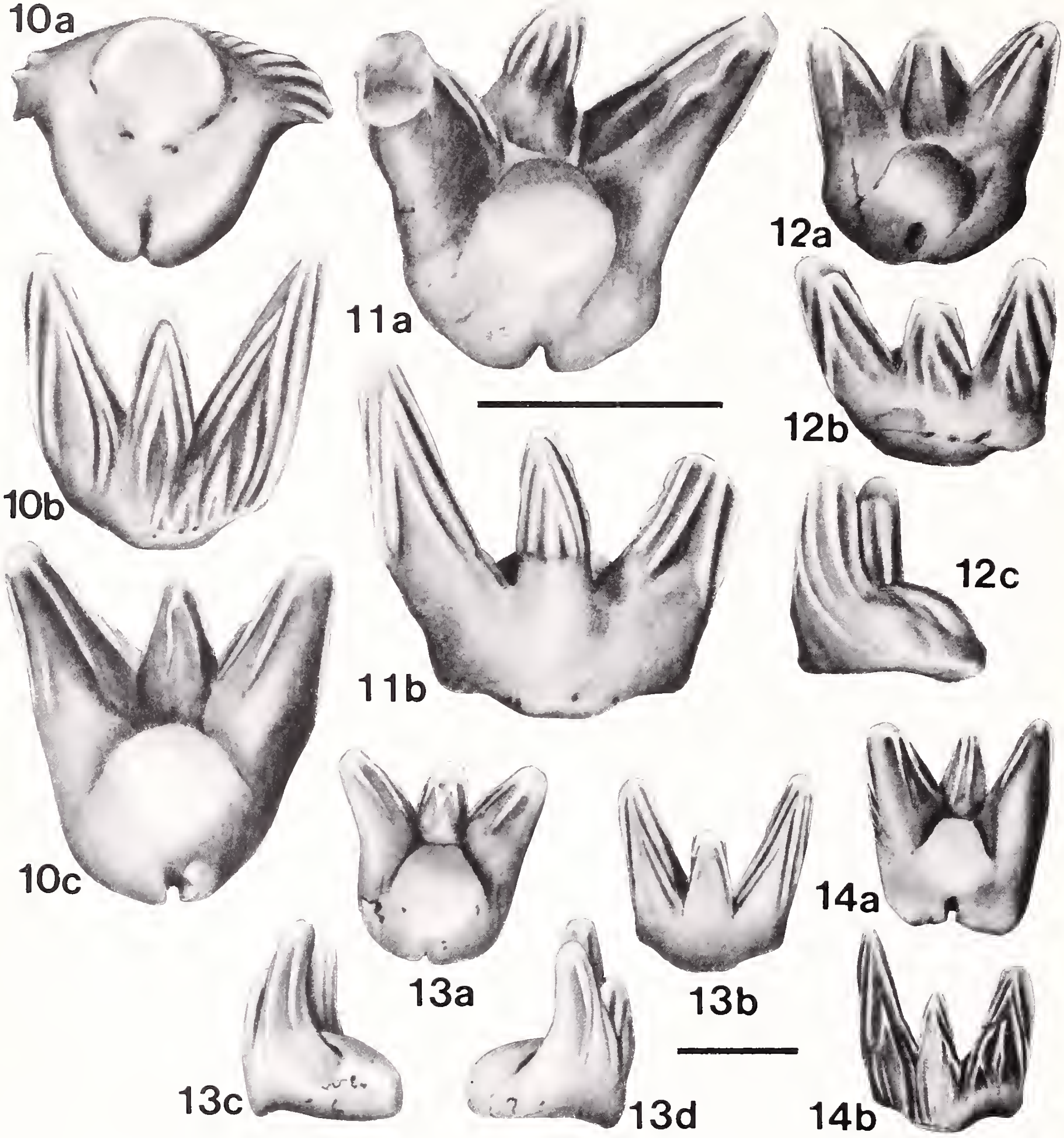
The pattern on the labial side of the tooth is often very faint or nearly absent. In at least one tooth (Fig. 8b) the pattern apparently never did occur in the proximal region of the labial side. In the other examples, however, the obscuration has probably resulted from abrasion by transport after the teeth were shed (Figs. 9, 11).

Discussion.—Except for the lingual foramen, the roots in *Xenacanthus*? *nebraskensis* teeth are similar to those in the Early Permian *X. luedersensis* (Johnson, 1979). The size and shape of the root of *X.*? *nebraskensis* teeth are also similar to those of *X. luedersensis* teeth. However, the relative root dimensions of *X.*? *nebraskensis* are quite the reverse of other well known *Xenacanthus* species. The average l-l/am-pl ratio of the *X.*? *nebraskensis* teeth is 0.92 (n = 50); it is 1.17 for *X. luedersensis* (n = 752; based on weighted means for 10 samples; see Johnson, 1979) and 1.48 for the Late Triassic *X. moorei* (n = 81; Johnson, 1980).

The principal cusps of *X.*? *nebraskensis* are remarkably symmetrical in stature as compared to other xenacanthodiid teeth (Johnson, 1979). The proximal end of the intermediate cusp is rather stout, not at all like its long, slender, cylindrical counterpart in *X. moorei* or even in the medial teeth (Johnson, 1979) of the much larger species of *Orthacanthus*. The pattern of the cristae on all three cusps is similar to that on the principal cusps of *X. luedersensis* and *X. moorei*, except that the cristae do not extend onto the labial margin of the root in these species.

Two main characters distinguish *X.*? *nebraskensis* teeth from all other Late Pennsylvanian and younger xenacanthodiid teeth I have examined (Johnson, 1979): the proximally compressed cristate intermediate cusp, and the extension of the cristae onto the root. It is namely the first feature that gives a reason to question the generic assignment. A cristate intermediate cusp seems to be a distinguishing feature of *Thrinacodus* teeth, as I interpret them. However, the teeth of that genus apparently have an apical button that is isolated from the cusps (for example, see Hussakof and Bryant, 1918, Pl. 44, figs. 3a and 3b, and the discussion above). If that is so, then the teeth described here cannot be placed in *Thrinacodus*, and may eventually have to be placed in a genus separate from it and *Xenacanthus*. Additional Devonian and Early Carboniferous specimens must be studied before a final definite generic assignment becomes possible. Other than these differences, the teeth described here are typical of the genus *Xenacanthus*.

To my knowledge, only one other species, *Bransonella tridentata* Harlton (1933), possesses characters that somewhat parallel those of *X.*? *nebraskensis*. It is based on a single specimen (National Museum of Natural History, NMNH 85529) from the Lower Pennsylvanian of southeastern Oklahoma, and was described by Harlton as a conodont. Zidek (1972, 1973) pointed out, however, that this is a xenacanthodiid tooth (Fig. 15a–c). Although the intermediate and one of the principal cusps are broken, it is obvious that the principal cusps are of nearly equal height and the intermediate cusp is only slightly shorter; all the cusps are coarsely cristate. The cristae extend onto the labial margin of the root and have a distinct spiral pattern (Fig. 15b). On the broken principal cusp they curve toward the intermediate cusp, but turn away from the cusp on the other principal cusp. There are six cristae per cusp. The principal cusps are of the same shape and stature as those of *X.*? *nebraskensis*, but are not as proximally compressed. The transverse major axis at the proximal end is parallel to the labial margin of the root (Fig. 15a). The intermediate cusp is compressed as in *X.*? *nebraskensis*. The root of *B. tridentata* is longer (am-pl length = 1.07 mm) than wide (l-l width = 0.86 mm). Whether or not the broad lingual



Figs. 10–14.—*Xenacanthus*? *nebraskensis*, new species, teeth from Site 3, Peru local fauna; both upper (Figs. 10–12) and lower (Figs. 13, 14) scale bars represent 1 mm; 38× and 19×, respectively. Fig. 10.—TMM 41648-140, paratype: a, basal, b, labial, and c, lingual-occlusal views. Fig. 11.—TMM 41648-139, paratype: a, lingual-occlusal, and b, labial views. Fig. 12.—TMM 41648-137, paratype: a, lingual-occlusal, b, labial, and c, am/pl views. Fig. 13.—TMM 41648-136, paratype: a, lingual-occlusal, b, labial, c and d, am/pl views. Fig. 14.—TMM 41648-138, paratype: a, lingual-occlusal, and b, labial views.

indentation is the result of an enlarged foramen is uncertain. The apical button (Fig. 15a) is in contact with this indentation, but is not in contact with the intermediate cusp, which may suggest this species belongs to *Thrinacodus*. It is essentially restricted to that area of the root lingual to the intermediate

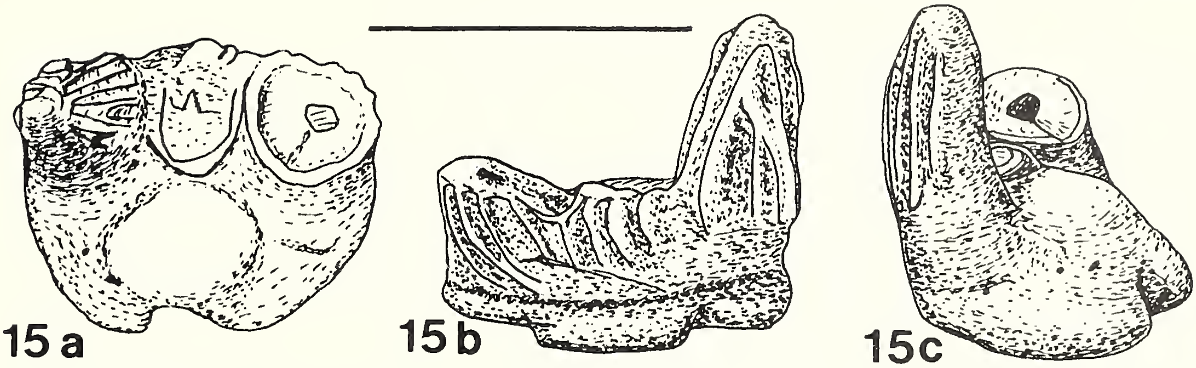


Fig. 15.—*Thrinacodus*? (*Bransonella*) *tridentata* tooth, NMNH 85529 (holotype), from the Lower Pennsylvanian of southeastern Oklahoma: a, occlusal, b, labial, and c, oblique am/pl views. Scale bar represents 1 mm. 42×.

cusp and is not in contact with the principal cusps. The basal tubercle (Fig. 15b) has a well defined labial margin. The differences between this species and *X.*? *nebraskensis* are not as great as between *X.*? *nebraskensis* and *X. luedersensis* or *X. moorei*. Differences between *X.*? *nebraskensis* and *B. tridentata* include the positions of the apical button, attitudes of the proximal transverse axis of the principal cusps, and possibly the lingual root margins.

The only other species that may be similar to *X.*? *nebraskensis* is "*Diplodus*" *minutus* Agassiz 1843, if it should prove to be a valid species. It was synonymized with *D. gibbosus* by Woodward (1889); however, this species probably belongs to *Orthacanthus* (see Johnson, 1979). "*D. minutus*" may include teeth with more than one intermediate cusp. A single tooth from the Peru Site 2 (Ossian, 1974) might conceivably belong to this species. This tooth (Fig. 16) has three relatively short (but equal) intermediate cusps with a corresponding elongate root. Otherwise, it is rather similar to the *X.*? *nebraskensis* teeth and is provisionally assigned to that species. It may have occupied a unique position in the tooth series (symphysis?) and may seem rare only because the total number of available teeth is low compared to the Waggoner Ranch Collection from north-central Texas (Johnson, 1979).

Since some of the better known vertebrate localities in North America and Europe occur in the Upper Pennsylvanian, it is surprising that teeth of the *X.*? *nebraskensis* type have not been reported before. Perhaps because of their small size, as in *X. luedersensis* (Berman, 1970), they have been overlooked. Despite the use of bulk sampling techniques, it is curious that Lund (1970, 1976) did not recover any similar teeth from units of similar age in the Dunkard Basin. *Orthacanthus compressus* is an equally common species in the Peru local fauna and it is also common in the Dunkard Basin. However, the Permo-Pennsylvanian species, *O. platypternus*, a stream inhabitant known from the Dunkard is absent in the Peru local fauna.

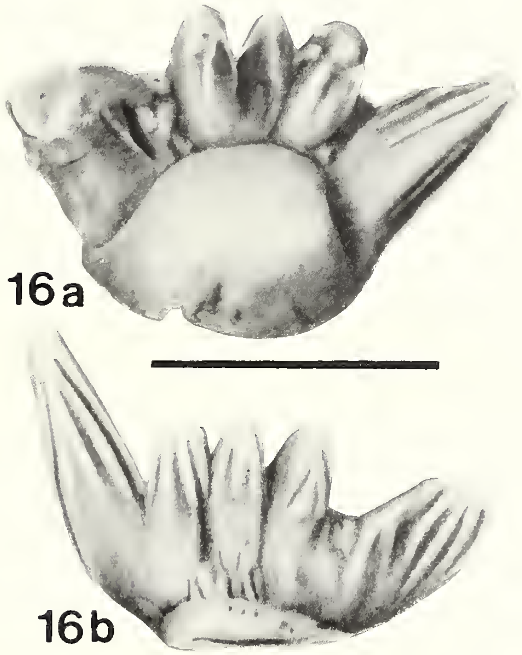


Fig. 16.—*Xenacanthus*? *nebraskensis*? tooth, TMM 41647-329, from Site 2, Peru local fauna: a, lingual-occlusal, and b, labial views. Scale bar represents 1 mm. 38×.

CONCLUSIONS

Teeth in the homodont dentition of *Xenacanthus*? *nebraskensis* possess characters of both *Xenacanthus* and *Thrinacodus*. The primitive nature of its intermediate cusp and its relatively late appearance preclude *X.*? *nebraskensis* or its presumed precursor, *T.*? (*Bransonella*) *tridentata*, from being ancestral to contemporary and younger species of *Xenacanthus*. The *Thrinacodus-Xenacanthus* lineage more likely developed through a series of other species starting in the Late Devonian (Johnson, 1979, text-fig. 48).

In view of the distribution of other contemporary xenacanthodiid species, the single occurrence of *X.*? *nebraskensis* suggests that it may be a relict species. It may have been a stream inhabitant, as *Orthacanthus platypternus* was elsewhere, which might account for its restricted occurrence.

LITERATURE CITED

Agassiz, L. 1837–1844. Recherches sur les poissons fossiles. Neuchâtel. Pp. 1–390.

Berman, D. S. 1970. Vertebrate fossils from the Lueders Formation, Lower Permian of north-central Texas. Univ. California, Publ. Geol. Sci., 86:1–61.

Beyrich, E. 1848. Über *Xenacanthus decheni* und *Holacanthus gracilis*, zwei Fische aus der Formation des Rothliegenden in Nord Deutschland. Monatsb. Berlin Wiss. Akad., 1848: 24–33.

Eastman, C. R. 1899. Description of new species of *Diplodus* teeth from the Devonian of northeastern Illinois. J. Geol., 7:489–493.

Fritsch, A. 1889. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, Vol. 2. F. Řivnáč, Prag, pp. 95–114.

———. 1895. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, Vol. 3. F. Řivnáč, Prag. Pp. 3–48.

Harlton, B. H. 1933. Micropaleontology of the Pennsylvanian Johns Valley Shale of the Ouachita Mountains, Oklahoma, and its relationship to the Mississippian-Caney Shale. J. Paleont., 7:3–29.

Hotton, N. 1952. Jaws and teeth of American xenacanth sharks. J. Paleont., 26:489–500.

Hussakof, L., and W. L. Bryant. 1918. Catalog of the fossil fishes in the Museum of the Buffalo Society of Natural Science. Bull. Buffalo Soc. Nat. Sci., 12:1–346.

Johnson, G. D. 1979. Early Permian vertebrates from Texas: Actinopterygii (*Schaefferichthys*), Chondrichthyes (including North American Pennsylvanian and Triassic Xenacanthodii), and Acanthodii. Unpublished Ph.D. dissertation, Southern Methodist Univ., Dallas. Pp. 76–289.

———. 1980. Xenacanthodii (Chondrichthyes) from the Tecovas Formation (Late Triassic) of west Texas. J. Paleont., 54:923–932.

Lund, R. 1970. Fishes from the Duquesne Limestone (Conemaugh, Pennsylvanian), Part I: Fossil fishes from southwestern Pennsylvania. Ann. Carnegie Mus., 41:71–101.

———. 1976. General geology and vertebrate biostratigraphy of the Dunkard Basin. Pp. 171–182, *in* The continental Permian in Central, West, and South Europe (H. Falke, ed.), D. Reidel Co., Dordrecht, Holland.

Newberry, J. S., and A. H. Worthen. 1866. Description of new species of vertebrates, mainly from the subcarboniferous limestone and Coal Measures of Illinois. Illinois Geol. Surv., 2:9–134.

Ossian, C. R. 1974. Paleontology, paleobotany, and facies characteristics of a Pennsylvanian delta in southeastern Nebraska. Unpublished Ph.D. dissertation, Univ. of Texas, Austin. Pp. 117–118.

Peyer, B. 1968. Comparative Odontology. Univ. Chicago Press, Chicago-London, 347 pp.

St. John, O., and A. H. Worthen. 1875. Descriptions of fossil fishes. Paleontology of Illinois, Illinois Geol. Surv., 6:245–488.

Simpson, G. G., A. Roe, and R. C. Lewontin. 1960. Quantitative Zoology, rev. ed. Harcourt Brace and Co., New York, 440 pp.

Woodward, A. S. 1889. Catalogue of the fossil fishes in the British Museum (Nat. Hist.), pt. 1. Taylor and Francis, London, 474 pp.

Zidek, J. 1972. Oklahoma paleoichthyology, Part I: A review and commentary. Oklahoma Geol. Notes, 32:171–187.

———. 1973. Oklahoma paleoichthyology, Part II. Elasmobranchii (*Cladodus*, minute elements of cladoselachian derivation, *Dittodus* and *Petrodus*). Oklahoma Geol. Notes, 33: 87–103.

Note Added in Proof

The *Thrinacodus* teeth could not be located when this study was in progress (Robert W. Purdy, personal communication). They have since been discovered, and found not to be similar to *Xenacanthus* teeth (Susan Turner, personal communication). They may not be xenacanthodiid teeth. The *D. incurvus* teeth are similar to the elasmobranch *insertae sedis* teeth illustrated by Turner (1982:118–124; J. Vert. Paleontol., 2:117–131; 1983, 3:38).

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